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# A Potent Analog of Recombinant Bovine Somatotropin Accelerates Growth in Juvenile Coho Salmon (*Oncorhynchus kisutch*)

N. E. (Ted) Down, Edward M. Donaldson, and Helen M. Dye

*Department of Fisheries and Oceans, Biological Sciences Branch, West Vancouver Laboratory, West Vancouver, B.C. V7V 1N6*

and Thomas C. Boone, Keith E. Langley, and Lawrence M. Souza

*AMGen, 1900 Oak Terrace Lane, Thousand Oaks, CA 91320, USA*

Down, N. E., E. M. Donaldson, H. M. Dye, T. C. Boone, K. E. Langley, and L. M. Souza. 1989. A potent analog of recombinant bovine somatotropin accelerates growth in juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 46: 178–183.

Recombinant bovine somatotropin and a recently engineered analog of bovine somatotropin were compared for their growth-promoting ability in underyearling coho salmon (*Oncorhynchus kisutch*). Treated fish were given five biweekly intraperitoneal injections of one of the hormone preparations at either 0.2 or 2.0 μg/g body weight. Both substances significantly enhanced growth, and by the end of the treatment period the fish injected with the high dose of the analog were significantly larger than all other groups, being 43.5% heavier than the sham-treated (saline injected) fish. Fish treated with the high dose of the native form of somatotropin were 25.3% heavier than the sham-treated group, but were not significantly different in size from fish treated with the low dose of analog. A four-point bioassay indicated that the analog had approximately nine times the growth-promoting potency of the native form of bovine somatotropin in coho salmon. Food conversion efficiency was improved by somatotropin therapy, but all groups exhibited a similar osmoregulatory capacity when subjected to a 24-h seawater challenge during the posttreatment period. Given the economic feasibility of producing recombinant proteins in large quantities, this analog has the potential to improve the production characteristics of cultured salmon.

On a comparé une somatotrophine bovine recombinante à un analogue de la somatotrophine bovine de fabrication récente, au point de vue de leur action stimulante sur la croissance chez le saumon coho (*Oncorhynchus kisutch*) de moins d'un an. Les poissons traités ont reçu cinq injections intrapéritonéales bi-hebdomadaires d'une des préparations hormonales à raison de 0,2 ou de 2,0 μg/g (poids corporel). Les deux préparations ont stimulé de façon significative la croissance des poissons; à la fin du traitement, ceux qui avaient reçu l'analogue à dose élevée étaient beaucoup plus gros que ceux des autres groupes, leur poids étant supérieur de 43,5 % à celui des poissons soumis au traitement fictif. Le poids des poissons recevant la dose élevée de somatotrophine naturelle était de 25,3 % plus élevé que celui des poissons soumis au traitement fictif, mais leur grosseur ne différait pas dans une mesure significative de celle des poissons recevant la faible dose d'analogue. D'après les résultats d'une épreuve biologique en quatre points, l'action stimulante de l'analogue sur la croissance est à peu près neuf fois plus puissante que celle de la somatotrophine bovine naturelle chez le saumon coho. Le traitement à la somatotrophine a amélioré le rendement de la conversion alimentaire, mais le pouvoir d'osmorégulation, évalué dans une épreuve de 24 h en eau salée après le traitement, était le même pour tous les groupes. Étant donné que la production massive de protéines recombinantes est économiquement réalisable, l'analogue pourrait être utilisé pour améliorer les caractéristiques de production du saumon d'élevage.

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Growth rate and food conversion efficiency are critical aspects in the economics of finfish aquaculture (Gill et al. 1985; Donaldson 1986). In an earlier series of experiments conducted in this laboratory (review Donaldson et al. 1979), it was shown that administration of native bovine growth hormone accelerated growth and improved food conversion in juvenile Pacific salmon, thus demonstrating that the availability of endogenous somatotropin limits somatic growth of salmonids. We were also able to demonstrate that both recombinant bovine and recombinant avian somatotropins were equipotent with native bovine somatotropin when administered to juvenile coho salmon (*Oncorhynchus kisutch*) (Gill et al. 1985).

Recently, the in vivo biological potency of certain hormonal peptides has been dramatically enhanced by the deletion, substitution, or addition of specific amino acids with the net effect of increasing either resistance to degradation or receptor binding efficacy. For example, analogs of mammalian and teleostean gonadotropin-releasing hormones, which contain specific amino acid substitutions, are superactive in their effects on cyprinids and salmonids (Peter et al. 1985; Van Der Kraak et al. 1987).

Attention is now turning to the larger and more complex peptide hormones. For example, genetic engineering techniques have been used to produce a concensus alpha-interferon which contains those amino acids which most frequently occur in a series of natural alpha-interferons and which has a higher potency than any of the individual natural sequences upon which

its structure was based (Alton et al. 1983). Recently, a potent analog of bovine somatotropin was developed that differs from the natural somatotropin in that seven amino acids have been deleted. The deletion in this engineered analog of bovine somatotropin occurs in the same region as a 15 amino acid deletion found in the naturally occurring 20 000-dalton (20K) variant of human growth hormone. The human 20K variant and the more common 22 000-dalton (22K) molecules have similar biological activities, when tested for growth promotion in hypophysectomized rats (Lewis et al. 1978). Nonhuman 20K variants have not been identified.

The purpose of the current study has been to compare the potency of this recombinant bovine somatotropin analog with recombinant bovine somatotropin (native form) in juvenile coho salmon.

## Materials and Methods

### Experimental Animals

Juvenile coho salmon of the 1984 brood year were obtained from the Capilano Salmon Hatchery (North Vancouver, B.C.) on 16 July 1985. Individuals in the range 2.2–3.0 g (2.6 g ± 0.6 SD) were selected and randomly assigned to one of 14 aquaria until each contained 60 fish. Each of the flow-through aquaria was supplied with aerated well water at 10.8°C (±0.25 SD) and a simulated natural photoperiod was provided. Salmon were acclimated to these conditions for 8 d before the experiment began. Fish were housed in 50-L aquaria initially but, because of their rapid growth, were transferred to 200-L aquaria at week 4 of the experiment (on a scheduled sampling day) where they remained until the completion of the experiment. During the study, fish were hand-fed, twice daily to satiation, a commercial semimoist diet (Oregon moist pellets). Individual records of food consumption were kept for each experimental tank to allow for the comparison of food conversion efficiency for each of the experimental groups.

### Hormones

Two somatotropins based on the bovine gene were used in this experiment. The first was recombinant bovine somatotropin (22K-rbGH Lot 217-1). The amino acid sequence of this 22K molecule is identical to pituitary-derived bovine somatotropin and its preparation has been described previously (Langley et al. 1987). Lot 217-1 was lyophilized from a solution containing 0.03 M $NaHCO_3$, 5.84 mM lactose, and 11.0 mM mannitol, pH 8.5. The final product contained 19.3% hormone by weight and was greater than 95% pure as estimated by SDS–polyacrylamide gel electrophoresis (PAGE).

The second somatotropin tested was a newly developed analog of the 22K-rbGH molecule with a molecular weight of approximately 21 000 (21K-rbGH Lot 252). This variant form of bovine somatotropin was derived from a synthetic gene lacking the nucleic acid information for amino acids 33–39 and is approximately twofold more potent than 22K-rbGH in a hypophysectomized rat bioassay (L. M. Souza, unpubl. data). The analog was isolated from *Escherichia coli* and purified in the same manner as that described for 22K-rbGH (Langley et al. 1987). Lot 252 was lyophilized from the same buffer constituents as Lot 217-1. The final product contained 13.3% hormone by weight and was greater than 95% pure as estimated by SDS–PAGE.

Two doses of each hormone (0.2 and 2.0 μg/g) were administered every second week. Previous work in our laboratory with native forms of somatotropin indicated that the lower of these two doses would be near the lower threshold of effectiveness and that the higher dose would produce a submaximal growth response. It was important not to exceed the minimum dose required to achieve the maximum effect, as the potency comparison would have been biased. Both hormones were dissolved in distilled water to provide a stock solution of 1.0 μg somatotropin/μL. For the initial treatment, the stock was further diluted to 0.026 or 0.26 μg/μL and each fish was given a 20-μL intraperitoneal injection using a Hamilton P-600 dispenser fitted with a 1.0-mL syringe and 30-gauge needle. Hormone concentration was adjusted for subsequent injections to compensate for growth. For the last two treatments the injection volume was increased to 50 μL and the hormone was delivered via a Socorex dispenser fitted with a 27-gauge needle. Saline-injected control fish received an equal volume of 0.01 M $NaHCO_3$, 0.15 M NaCl, and 1.0% bovine serum albumin (BSA).

### Experimental Protocol

Seven experimental groups were defined for this study. These included fish tested with each of the two hormones at two doses, a saline-injected (sham) control group, an uninjected control (which were weighed and measured on routine sampling days but never injected), and an "unhandled" control group (which were weighed and measured at the start of the experiment and not handled again until week 10, the end of the treatment period).

There were two replicates of each experimental group consisting of 60 fish each. Experimental tanks were arranged in two rows, and within each row, the assignment of treatment to tank was random with the following exception. The unhandled control group was placed in the tanks at the least disturbed end of each row. This allowed us to test whether the unhandled fish, with the minimum possible disturbance, were of a significantly different size (at the end of the experiment) with respect to the control fish which were handled on a regular basis.

Fish were sampled, in random order, at the start of the experiment (week 0) and every 2 wk thereafter for 12 wk. After being anaesthesized in 0.05% 2-phenoxyethanol, each fish was weighed to the nearest 0.1 g and fork length was determined to the nearest 0.1 cm. Fish were injected with the appropriate hormone or saline solution on the first five sampling dates. At week 10, the fish were sampled normally (including the unhandled controls), but every third fish was killed by over-anaesthesia and frozen (approximately 40 fish/treatment). These fish were oven-dried at 85°C for a minimum of 24 h, which provided a sample for percent moisture determinations. At week 12, the remaining fish were sampled for weight and length and fish from each tank within a treatment group were pooled into a single 200-L tank. In the period between weeks 13 and 14, 18 fish were randomly selected from each treatment group and submitted to a seawater challenge (Blackburn and Clarke 1987). Fish subjected to this test were transferred directly from freshwater into ambient seawater. Blood sodium levels for these fish were determined, using a flame photometer, 24 h after the transfer. Under these conditions, blood sodium is indicative of a salmon's seawater osmoregulatory capability (Blackburn and Clarke 1987). The remaining fish were held until week 23 when a final set of weight and length data was collected.

### Statistical Analysis

Data were log transformed to meet the assumptions of normality and homogeneity of variance. Unless otherwise stated the 99% confidence level ($p < 0.01$) was used to determine significant differences between treatments. The statistical analysis system (SAS, version 4) was used for ANOVA calculations and the least square means multiple comparison was used to identify treatment differences.

Length and weight data for each treatment group were compared by one-way ANOVA at each sampling date. As a preliminary analysis indicated that tank row was not a significant factor, the data were pooled for each tank within a treatment. Condition factor (CF) was determined by the formula CF = (weight/length$^{3.08}$)100. The exponent 3.08 was determined by regressing log weight on log length for all data points. The relationship was highly linear ($r^2 = 0.98$) with a slope of 3.08. One-way ANOVA was used to compare CF between all treatment groups at each sampling time and within each group across all sampling times.

After the week 8 sampling period, the accidental loss of one experimental tank being treated with the high dose of 22K-rbGH eliminated the tank replication within this treatment group. For this reason, several of the calculations, such as specific growth rate, food conversion rate, and the four-point bioassay, used week 8 as the endpoint of the experiment. Specific growth rate was determined over weeks 0–8 for both weight and length by $(\ln V_1 - \ln V_0)/(t_1 - t_0) \times 100$ where $\ln V_1$ and $\ln V_0$ are the natural logarithms of weight or length at the end of the time interval ($t_1$) or the start of the time interval ($t_0$), respectively (Higgs et al. 1975). Food conversion efficiency for this same period was determined by dividing the total dry weight gain of fish by the dry weight of food consumed ($\times 100$) for each treatment group. Specific growth rate and food conversion efficiency could only be calculated on the mean results recorded for each tank of fish. With two tanks per treatment, there was not a sufficient measure of variance available to compare the effect of treatment on these factors statistically.

The relative potency of the 21K somatotropin analog relative to the native 22K form was estimated using the EXBIOL computer package for four-point bioassay (Sakiz and Guillemin 1962). This analysis was run on the week 8 data and used the sham-treated control group as the reference group.

## Results

There were no significant differences in fish size (weight or length) at the onset of the experiment (Fig. 1A, 1B). The untreated control fish were similar in size to the sham-treated fish over the course of the experiment except that at weeks 6 and 8 the former were significantly larger. This was a transient situation, and by week 10, no significant size differences were noted for any of the control groups, including the group which had not been handled (unhandled controls) since the initiation

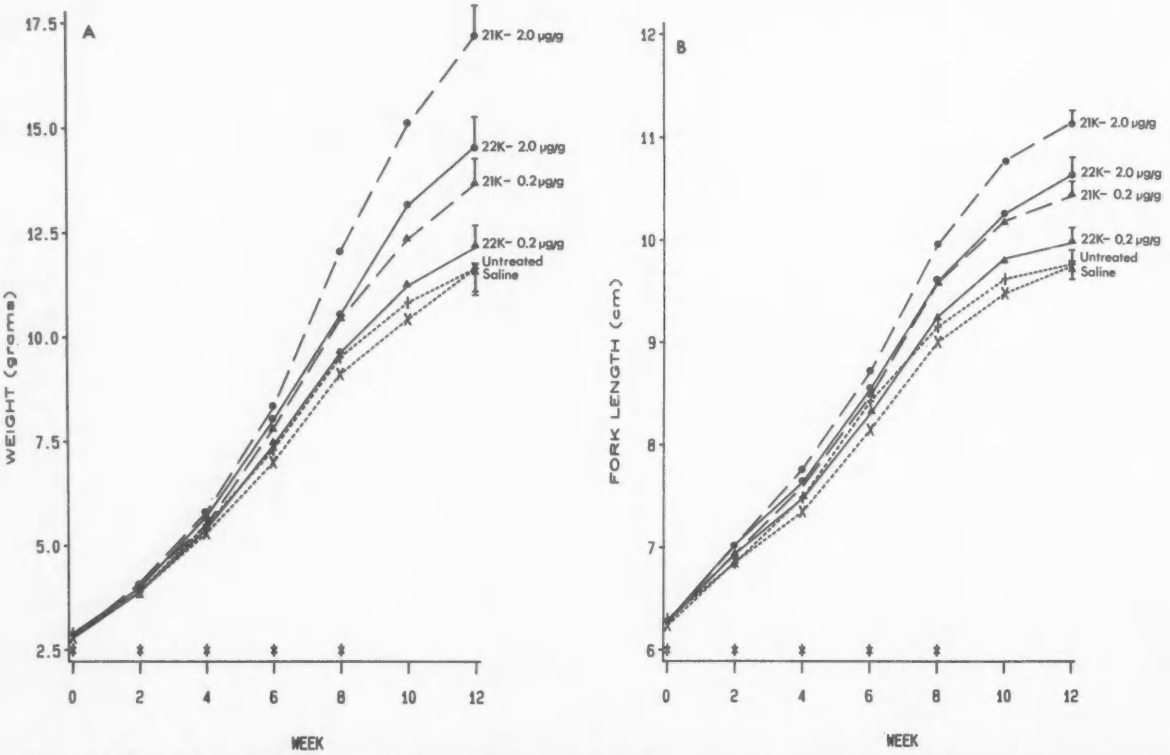


FIG. 1. (A) Mean weight or (B) fork length of each experimental group over the first 12 wk of the experiment. For clarity, 2 standard errors are indicated for week 12 data only. Fish were either untreated, given five intraperitoneal (ip) injections of a saline solution (saline), or given five ip injections of a somatotropin solution. Injection dates are indicated by an asterisk. Recombinant bovine somatotropin (22K) and a 21 000-Dalton analog (21K) were tested at the two dose levels indicated.

TABLE 1. Summary statistics for specific growth rate (SGR), food conversion efficiency (FCE), percent whole body moisture, and plasma sodium levels for the six experimental groups.

| Experimental group | SGR (%/d) (weeks 1–8) Weight | SGR (%/d) (weeks 1–8) Length | FCE (weeks 1–8) (%) | Moisture (%) | Plasma $Na^+$ (meq/L)[a] |
|---|---|---|---|---|---|
| 1. Control | 2.16 | 0.67 | 26.4 | 71.2 | 169.2 |
| 2. Sham | 2.11 | 0.65 | 29.1 | 72.3 | 170.2 |
| 3. 22K-rbGH, 0.2 μg/g | 2.17 | 0.70 | 30.6 | 72.2 | 171.4 |
| 4. 22K-rbGH, 2.0 μg/g | 2.30 | 0.76 | 31.7 | 72.7 | 168.9 |
| 5. 21K-rbGH, 0.2 μg/g | 2.34 | 0.76 | 31.7 | 73.3 | 170.8 |
| 6. 21K-rbGH, 2.0 μg/g | 2.60 | 0.83 | 33.2 | 73.0 | 169.3 |

[a]After a 24-h seawater challenge.

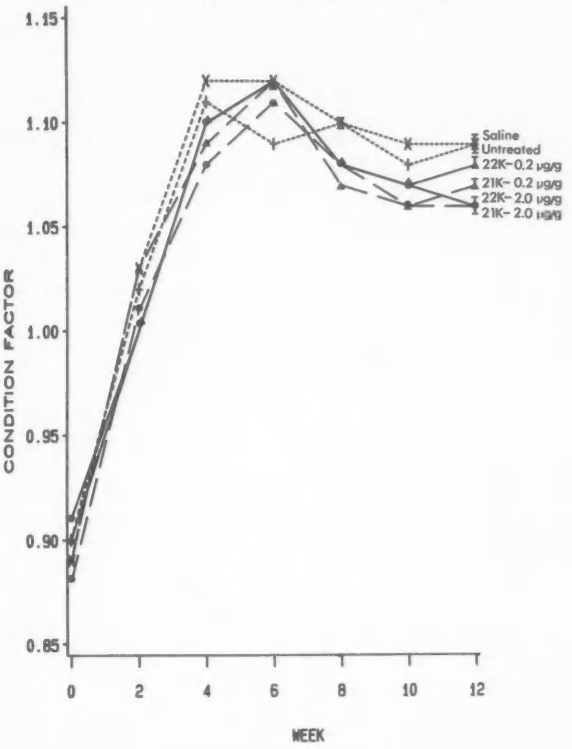


FIG. 2. Mean condition factor for each experimental group over the first 12 wk of the experiment. See legend to Fig. 1 for an explanation of abbreviations. One standard error is indicated for each group at week 12.

of the experiment. By the end of the treatment period (week 10), all of the somatotropin treated groups were significantly larger (as measured by weight or length) than were the untreated or sham-treated control fish. At this time the group treated with the high dose of 21K-rbGH was significantly larger than all other experimental groups (Fig. 1). The groups injected with a low dose of 21K-rbGH or a high dose of 22K-rbGH were not of a significantly different size from one another at week 10 (or at any other time over the course of the experiment); however, both were significantly larger than the low-dose 22K-rbGH treated group. This latter group was significantly larger than the control groups at week 10 but not during previous weeks. At week 23 the relationships between experimental groups were essentially unchanged except that the low-dose 22K-rbGH group was no longer significantly larger than the two control groups. There were no significant differences in percent moisture when fish from the six experimental groups were compared at week 10 (Table 1), indicating that the observed differences in weight reflected changes in tissue mass and not fluid uptake.

CF at the start of the experiment were similar for all groups (Fig. 2). A rapid and significant increase in CF was observed for all groups over the first 4–6 wk. During the remainder of the experiment, CF declined in all groups but more sharply in the somatotropin-treated fish. From weeks 8 to 12, all hormone treated groups had significantly lower CF than did the control groups. By week 23 there were no significant effects of treatment on CF.

The specific growth rates and food conversion efficiencies were highest in the group treated with the high dose of 21K-rbGH (Table 1). The relationships observed between the other experimental groups reflect the differences in size attained by the various groups over the course of the experiment.

The results of the four-point bioassay indicated that, for length, all levels of somatotropin significantly enhanced growth and that the potency ratio of the 21K-rbGH analog to the 22K-rbGH native form was 9.02 (confidence limits 4.18, 28.6). For weight data, all treatments with the exception of the low dose of 22K-rbGH significantly enhanced growth and the potency ratio of analog to native form was 8.58 (confidence limits 3.89, 28.7).

The 24-h seawater challenge revealed no significant differences in osmoregulatory capacity between any of the experimental groups (Table 1). The mean plasma sodium concentration was 170 mEq/L ($\pm 0.91$ SD).

## Discussion

Pituitary-derived mammalian somatotropins are well-documented enhancers of teleost growth (Donaldson et al. 1979). Recently, recombinant bovine somatotropin, cultured in *E. coli*, has been shown to be equipotent to pituitary-derived (native) bovine somatotropin in its ability to enhance the growth of coho salmon (Gill et al. 1985). The recombinant somatotropin used in that work was identical in primary structure to native bovine somatotropin and was the same material identified as 22K-rbGH in the present work. The 21K-rbGH analog is approximately twofold more potent than the 22K form when tested in a hypophysectomized rat bioassay (L. M. Souza, unpubl. data) and the data presented here represent the first potency comparison of this material in fish.

The present experiment indicates that the 21K analog is approximately nine times more potent than the native form, in coho salmon. Even if we accept only the lower fiducial limit,

the analog has more than three times the growth-enhancing potential of unaltered bovine somatotropin. The mechanism of this improved action has not yet been elucidated. The analog may have a longer residency time on receptors or it may have a longer biological half-life. Less likely is the possibility that the analog resembles endogenous salmon somatotropin more than 22K-rbGH, thereby improving recognition and binding to receptors.

In humans, a naturally occurring 20K form of growth hormone is a genetic variant of the more common 22K molecule and has 15 amino acid deletions extending from positions 32 to 46 (Lewis et al. 1980). This fully encompasses the seven deletions at positions 33–39 we have described for 21K-rbGH. The 20K human growth hormone variant has full or somewhat reduced growth-promoting activity in hypophysectomized rats, but greatly reduced in vitro insulin-like activity when compared with 22K human growth hormone (Lewis et al. 1987; Kostyo et al. 1987). In human subjects, the 20K variant has diminished free fatty acid suppressing activity (Culler et al. 1988). Effects of the 21K-rbGH analog on carbohydrate or lipid metabolism have not been investigated.

Previous attempts to synthesize somatotropin molecules with fewer amino acids have generally led to a significant loss of biological activity. Li et al. (1969) produced a version of human growth hormone with three amino acid deletions and a misplaced tryptophan residue that had only 10% of the growth-promoting activity of the native hormone. Donaldson et al. (1979) reviewed this topic and suggested that the tertiary structure of somatotropin is probably critical to its biological action and that shortened segments of the whole molecule are not likely to have the same potency as the unaltered hormone.

In the present potency comparison it was necessary to choose dose levels of somatotropin that would provide a submaximal response. The degree of increased potency that we observed with the analog was unexpected, and if we have exceeded the minimum dose required to produce a maximal effect, then the potency difference between the hormone forms would be underestimated. The specific growth rate that we have recorded for the fish treated with 2 μg 21K-rbGH/g every 2 wk (2.60%/d for weight) somewhat exceeds that reported by Gill et al. (1985) for similar sized coho salmon treated weekly with 5 μg rbGH/g (2.38%/d) or that reported by Higgs et al. (1976) for coho salmon treated weekly with 10 μg bovine GH/g (2.23%/d). Higgs et al. (1975) utilized weekly doses of bovine growth hormone as high as 100 μg/g without producing a substantially larger growth response. The rate observed in the present work may, therefore, be near maximal.

The marked increase in CF noted for all groups during the first several weeks of this study may be a result of the transfer of these fish from a large-scale culture situation into experimental conditions where factors such as density, feeding, and water quality may have been more optimal. However, it became evident that the CF of somatotropin-treated fish was lower than that of untreated fish over the latter half of the treatment period. This phenomenon has been recorded previously for Pacific salmon (Donaldson et al. 1979; Down et al. 1988a). In the present study, as in earlier studies (reviewed by Down et al. 1988a)), the effect of somatotropin treatment on linear growth was noted before an effect on weight gain became evident. This was probably due to direct and/or indirect effects of somatotropin on bone growth. The result of this earlier effect on length is a decline in CF. Differences in CF were not evident when the final (week 23) set of size measurements were taken. This indicates that the effect on CF is transient and will diminish after a suitable withdrawal period.

There was also an apparent relationship between the level of somatotropin-induced growth enhancement and food conversion efficiency. This effect has also been recorded for salmonids treated with various somatotropins (Donaldson et al. 1979; Gill et al. 1985). Markert et al. (1977) have reviewed possible physiological mechanisms which may account for the improved food conversion rates observed when somatotropin is administered to fish. As food costs generally represent the largest single expenditure for aquaculture operations, an improvement in the efficiency of food utilization has obvious practical benefits.

Several workers have indicated that somatotropin may play an integral role in the physiology of anadromous salmonids preparing to enter salt water (Clarke et al. 1977; Miwa and Inui 1985; Sweeting et al. 1985; Bolton et al. 1987; Richman et al. 1987). When we challenged fish with full-strength seawater, both control and treated groups were able to regulate blood sodium levels at a normal level expected for smolting salmon despite the fact that they would not normally be expected to smolt for approximately 6 mo. Size plays an important role in smolting (Blackburn and Clark 1987), and in the present experiment, all of the groups demonstrated rapid growth rates. At the time of the seawater challenge in late October, even the control fish had apparently achieved sufficient size to enter salt water.

The potential for using recombinant somatotropin to accelerate the growth of cultured salmon has been suggested (Down et al. 1988a). This may allow the producer to obtain a larger product during a fixed production cycle or alternatively to reduce the time required to produce a salmon of a given market size. The advent of recombinant DNA technology should make the use of purified proteins, such as somatotropin, economically feasible. A major drawback to date is the absence of a practical way to administer these products on a large scale. Down et al. (1988b) have suggested that recombinant somatotropin may need to be injected every 1–2 wk to maintain effective plasma concentrations of hormone. If the 21K-rbGH analog does in fact have an increased half-life, it could be administered less frequently.

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# Evidence of Demic Structure for a Population of Yellow Perch (*Perca flavescens*)

S. K. Aalto

*Department of Mathematics and Computer Science, St. Francis Xavier University, Antigonish, N.S. B2G 1C0*

and G. E. (Buck) Newsome

*Department of Biology,*
*St. Francis Xavier University, Antigonish, N.S. B2G 1C0*

Aalto, S. K., and G. E. (Buck) Newsome. 1989. Evidence of demic structure for a population of yellow perch (*Perca flavescens*). Can. J. Fish. Aquat. Sci. 46: 184–190.

A number of authors suggest that yellow perch (*Perca flavescens* and *P. fluviatilis*) populations are composed of subpopulations which persist over various periods of time. If the period of time is sufficiently long, then subpopulations may be demes or stocks of perch. These observations are based on the results of tagging studies, comparative growth studies, and behavior patterns of yellow perch. In this paper, evidence is presented which provides additional support for demic structure of yellow perch populations. This evidence consists of yearly egg-mass counts over an extended period of time (1978–87) at a number of distinct sites in a study lake and trapping data by sex, age, and date during one spawning season (1984) at a number of distinct sites in the same lake. Several models concerning perch spawning behavior are introduced to provide a framework for analyzing the data. Analysis of the data not only provides support for demic models of perch population structure, but also provides an estimate of the separation of the demes (0.4–0.5 km).

Un certain nombre d'auteurs pensent que les populations de perchaudes (*Perca flavescens* et *P. fluviatilis*) sont composées de sous-populations qui persistent pendant des durées variables. Si la durée est assez longue, alors les sous-populations peuvent être des dèmes ou des stocks. Ces observations s'appuient sur les résultats d'études de marquage et d'études comparatives de la croissance ainsi que sur les types de comportement de la perchaude. Dans cet article, nous présentons des éléments qui viennent appuyer la notion d'une structure démique des populations de perchaudes. Nous présentons les résultats de dénombrements annuels des masses d'oeufs sur une grande période (1978–87) et à un certain nombre d'endroits distincts dans un lac d'étude ainsi que les données de capture par sexe, âge et date au cours d'une saison de fraie (1984), à un certain nombre d'endroits distincts dans le même lac. Différents modèles s'appliquant au comportement de fraie de la perchaude sont présentés de façon à constituer un cadre de travail pour l'analyse des données. Cette dernière vient non seulement confirmer les modèles démiques de structure des populations de perchaudes, mais fournit également une évaluation de la séparation des dèmes (0,4–0,5 km).

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A deme or stock is an intraspecific group of randomly mating fish which exhibit a significant degree of reproductive isolation from other demes or stocks (Ricker 1972; Altukhov 1981; Horrall 1981; Ihssen et al. 1981; Krebs 1985). Reproductive isolation can be maintained by either temporal or spatial separation during spawning, but members may freely mix with fish of other demes at other times during their life cycles.

A large number of investigators of both the North American yellow perch (*Perca flavescens*) and the Eurasian perch (*P. fluviatilis*) report evidence which suggests that they may exhibit demic structure. A variety of tagging studies indicate that perch, at least the mature ones, move very little from the region where initially tagged and show a high degree of site fidelity from year to year (Rodeheffer 1941; Mansuetti 1960; Muncy 1962; Williams 1965; Stobo 1971; Fortin and Magnin 1972; Nakashima and Leggett 1975; Kelso and Ward 1977; Clady 1977; Collette et al. 1977; Lind 1977; Thorpe 1977; Willemsen 1977). Other studies show that perch from different regions of the same body of water exhibit significant differences with respect to growth (Chikova 1973; Fortin and Fournier 1977; Nelson and Walburg 1977; Viljanen and Holopainen 1982) or other biological features such as meristics (Chikova 1973). These reports indicate that perch form relatively cohesive assemblages, particularly at spawning time, but these studies do not indicate that perch return to the region where they were initially spawned which is a prerequisite for demic structure.

In this paper we report additional evidence and provide analyses which strongly suggest that the population we are studying consists of separate local populations which are demes. Our evidence consists of egg-mass counts conducted at a number of distinct sites in the study lake over a 10-yr period and trapping studies made during one spawning season. Our analyses involve three commonly considered models of perch spawning site

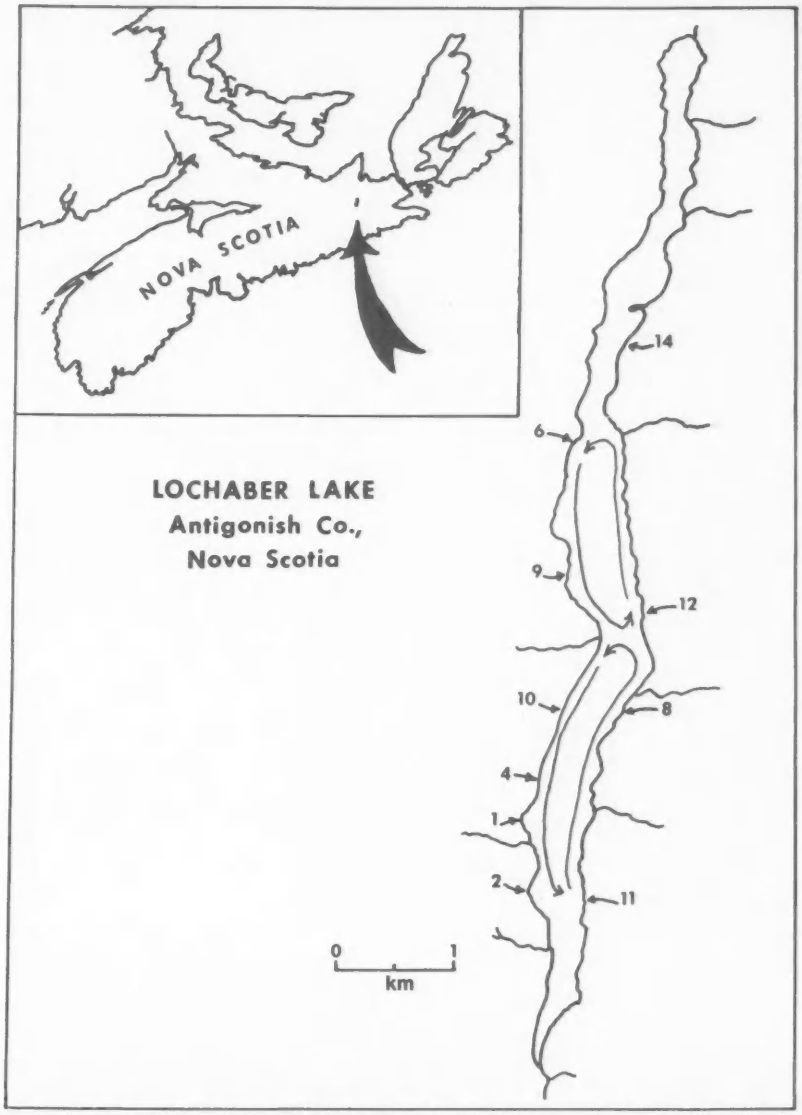


FIG. 1. Location of the study lake and the sample sites used in these investigations, and the directional flows of the two major circulations in the study lake.

selection behavior: random spawning site selection by each perch each spawning season; random spawning site selection by each first-time spawner and return to their initial spawning site for all other spawners; and return to the natal spawning site by each spawner (the demic model). Using our evidence, we are able to reject the first two of these models and further show that the evidence we have found is consistent with the third model.

## Materials and Methods

The population of yellow perch being studied inhabits Lochaber Lake which is a relatively long (8.4 km), narrow (0.7 km at its widest point), extremely oligotrophic lake, located in the northeastern part of mainland Nova Scotia (Fig. 1). We have been tracking the annual changes in abundance of egg-masses since 1978 using a modification of the egg-mass census method (Newsome and Aalto 1987) first suggested by Zhakov (1962). Each mature female deposits a single readily identifiable egg-mass annually. Census counts can provide very reliable estimates of the abundance of the mature females. The egg-masses are protected from losses due to predation by mechanisms which are poorly understood (Newsome and Tompkins 1985; Diamond and Wakefield 1986).

Lochaber Lake perch spawn at various places in the lake between the depths of 4 and 12 m during a 2-wk period in June. Since there is little or no temporal separation possible for the yellow perch spawning in Lochaber Lake, the available mech-

TABLE 1. Trapping effort, expressed as number of traps per 24 h, for June 1984 by site and date in Lochaber Lake, N.S.

| | June 1984 date | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Site | 6 | 7 | 8 | 13 | 14 | 15 | 19 | 20 | 21 | 22 | 26 |
| 4 | | | | | 4 | 4 | 2 | 2 | 2 | 3 | |
| 6 | | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | | |
| 8 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 5 | |
| 12 | | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 5 | 5 |
| 14 | | | | 3 | 3 | 3 | 3 | 3 | 3 | | |

TABLE 2. Yellow perch egg-mass counts by site for 1978–87 along isobathic transects at the depths of 6, 8, and 10 m in Lochaber Lake, N.S.

| Site | 1978 | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 124 | 155 | 226 | 79 | 132 | 93 | 32 | 77 | 54 | 107 |
| 2 | 27 | 18 | 21 | 16 | 23 | 7 | 15 | 8 | 8 | 32 |
| 4 | 17 | 57 | 61 | 2 | 52 | 45 | 15 | 37 | 13 | 26 |
| 6 | 39 | 39 | 57 | 11 | 16 | 39 | 14 | 17 | 26 | 60 |
| 8 | 8 | 12 | 10 | 3 | 6 | 23 | 2 | 10 | 8 | 38 |
| 9 | 0 | 19 | 10 | 4 | 8 | 14 | 0 | 12 | 11 | 7 |
| 10 | 2 | 25 | 17 | 2 | 22 | 25 | 3 | 18 | 3 | 10 |
| 11 | 14 | 18 | 11 | 12 | 24 | 10 | 14 | 13 | 3 | 24 |

anism for maintaining distinct demes would be spatial, i.e. distinct spawning sites for each deme.

Between June 6 and 26, 1984, which overlaps the spawning season to a considerable extent (Newsome and Aalto 1987), mature perch were collected at five sites using Windermere traps (Worthington 1950; Bagenal 1972). Trapping (Table 1) at each site continued until approximately 100 mature female perch had been trapped. Since this collection was made during the spawning period, captured fish were readily sexed. Before returning the captured fish to the lake, a key scale was removed (Newsome and Aalto 1987) so that age determinations could be made. Multiple recaptures of males were frequent, while recaptures of females were rarer.

## Results

Table 2 gives the results of the annual egg-mass censuses made during 1978–87 at a number of isolated sites (Fig. 1) in Lochaber Lake. This table suggests that some sites are more preferred spawning sites, while others are used only sparingly. Statistical support for this suggestion is given in Newsome and Aalto (1987). To examine the null hypothesis that the entries in Table 2 are independent of the year and site or that there is no association between year and site, a chi-square test of independence was performed (Brieman 1973; Mood et al. 1974). An overall test showed a significant dependence or interaction between year and site ($p < 0.001$). To ensure that this statistic does not arise from one or two anomalous sites, the chi-square statistics for all possible pairs of the eight sites were computed. These results are presented in Table 3 and the null hypothesis regarding independence of spawning site utilization and year is rejected for all of the 28 pairs of sites but three (2 and 11, 4 and 10, and 9 and 10) at the 0.01 level. Thus, there is ample evidence for a conclusion that year and spawning site are not independent for most pairs of sites. This is illustrated in Fig. 2 which compares the asynchronous variations in the abundance of reproducing female perch at sites 2 and 10.

The results of trapping at a number of isolated spawning sites during June 1984 are given in Table 4. Because the daily captures of females were too few for reliable comparisons, only the male age distributions were used in analyses discussed below. Ages greater than 5 were also pooled. Examination of Table 4 indicates that over the course of the spawning period, June 6–26 (Newsome and Aalto 1987), within-site age distribution heterogeneity was extreme in more than half of the sites examined (sites 4, 6, 8, 12, and 14). A closer examination reveals that prior to the peak of spawning activity (June 13, 1984) the proportion of older males is much higher than during the peak of spawning activity (June 13–26, 1984). Where sufficient data are available (sites 6, 8, and 12), comparisons showed that within-site age distributions were homogeneous prior to the peak of spawning (June 13). Similarly, homogeneity of within-site age distributions (sequential pooling of some samples was used to give sufficient data for at least three separate time intervals in this period) was observed during the peak spawning period. But, with the exception of site 6, the age distributions before and during the peak of spawning were significantly different ($8.21 < \chi^2 < 19.33$, $0.001 < p < 0.042$). Age distributions throughout the sampling period for site 6 were homogeneous ($\chi^2 = 2.19$, $p = 0.902$).

To compare age distributions between sites, analyses were restricted to the period of peak spawning activity because we assume that during this time, all spawning males would be present. Sufficient data for these comparisons were available for sites 4, 6, 8, 12, and 14 which are compared on a proportional basis in Fig. 3. The age distribution of the male perch at site 6 was, by means of chi-square tests, significantly different from the other four sites ($p < 0.001$). In Fig. 3 the age distributions of sites 12 and 14 appear more similar to each other in that there is an indication of a dominant age 5 year-class. Also, age distributions for sites 4 and 8 appear somewhat similar and lack the dominant age 5 of sites 12 and 14. These pairs of similar

TABLE 3. Chi-square scores (probability of obtaining score) for all possible pairs of sites for the egg-mass data (see text) in Lochaber Lake, N.S.

| | Site | | | | | | |
|---|---|---|---|---|---|---|---|
| Site | 2 | 4 | 6 | 8 | 9 | 10 | 11 |
| 1 | 38 (0.00) | 50 (0.00) | 47 (0.00) | 77 (0.00) | 40 (0.00) | 48 (0.00) | 39 (0.00) |
| 2 | | 74 (0.00) | 34 (0.00) | 45 (0.00) | 56 (0.00) | 64 (0.00) | 9.9 (0.36) |
| 4 | | | 63 (0.00) | 60 (0.00) | 31 (0.00) | 10 (0.34) | 50(0.00) |
| 6 | | | | 21 (0.01) | 37 (0.00) | 58 (0.00) | 44(0.00) |
| 8 | | | | | 31 (0.00) | 40 (0.00) | 37(0.00) |
| 9 | | | | | | 17 (0.06) | 43(0.00) |
| 10 | | | | | | | 38(0.00) |

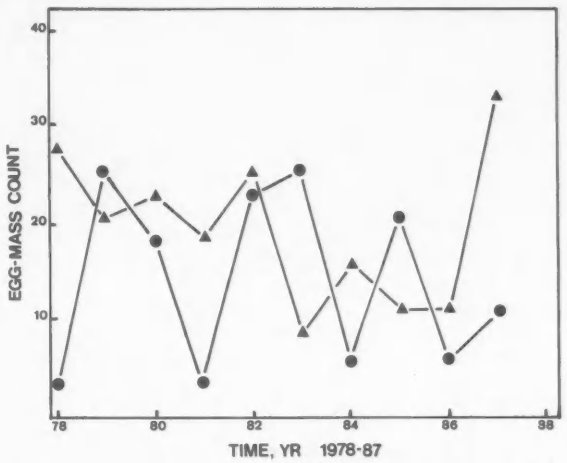


FIG. 2. Absolute changes in the perch egg-mass counts at site 2 (▲) and site 10 (●), Lochaber Lake, N.S., 1978–87.

TABLE 4. Captures of male yellow perch by date and site in Lochaber Lake, N.S.

| | | June 1984 date | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | Age | 6 | 7 | 8 | 13 | 14 | 15 | 19 | 20 | 21 | 22 | 26 |
| 4 | 3 | | | | | 122 | 52 | 0 | 35 | 6 | 8 | |
| | 4 | | | | | 56 | 26 | 0 | 11 | 0 | 7 | |
| | 5 | | | | | 44 | 22 | 0 | 5 | 6 | 6 | |
| | 6 | | | | | 9 | 8 | 0 | 0 | 0 | 0 | |
| | 7+ | | | | | 1 | 1 | 0 | 1 | 1 | 0 | |
| 6 | 3 | | 65 | 0 | 35 | 9 | 2 | 0 | 1 | 1 | | |
| | 4 | | 78 | 0 | 42 | 11 | 1 | 0 | 0 | 3 | | |
| | 5 | | 42 | 0 | 26 | 2 | 2 | 0 | 0 | 6 | | |
| | 6 | | 10 | 0 | 8 | 4 | 0 | 0 | 0 | 1 | | |
| | 7+ | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| 8 | 3 | 38 | 37 | 24 | 17 | 14 | 1 | 2 | 0 | 1 | 4 | |
| | 4 | 35 | 33 | 39 | 7 | 8 | 2 | 0 | 0 | 2 | 3 | |
| | 5 | 19 | 29 | 29 | 4 | 6 | 0 | 1 | 0 | 0 | 4 | |
| | 6 | 5 | 2 | 7 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | |
| | 7+ | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 12 | 3 | | 20 | 26 | 5 | 16 | 0 | 0 | 2 | 1 | 9 | 15 |
| | 4 | | 18 | 24 | 4 | 2 | 0 | 0 | 1 | 0 | 1 | 4 |
| | 5 | | 6 | 12 | 3 | 5 | 0 | 0 | 1 | 0 | 4 | 4 |
| | 6 | | 0 | 4 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 2 |
| | 7+ | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 14 | 3 | | | 27 | 26 | 5 | 0 | 4 | 17 | | | |
| | 4 | | | 33 | 7 | 3 | 0 | 2 | 5 | | | |
| | 5 | | | 21 | 13 | 2 | 0 | 3 | 5 | | | |
| | 6 | | | 6 | 1 | 1 | 0 | 0 | 2 | | | |
| | 7+ | | | 0 | 1 | 1 | 0 | 0 | 1 | | | |

sites were pooled and compared. Although not statistically different ($p = 0.072$), it is possible that the age distributions are distinct. These results indicate that there were at least two and possibly three different age distributions within the Lochaber Lake perch population.

## Discussion

The results of this investigation clearly demonstrate that year and spawning site selection are not independent among yellow perch inhabiting Lochaber Lake, N.S. The age distribution of male spawners at each site shows that early in the spawning season there are relatively more older perch than during the peak of spawning. There are two and possibly three distinct age distributions of male perch in Lochaber Lake. The following analyses of three models of perch spawning behavior provide support for the demic model.

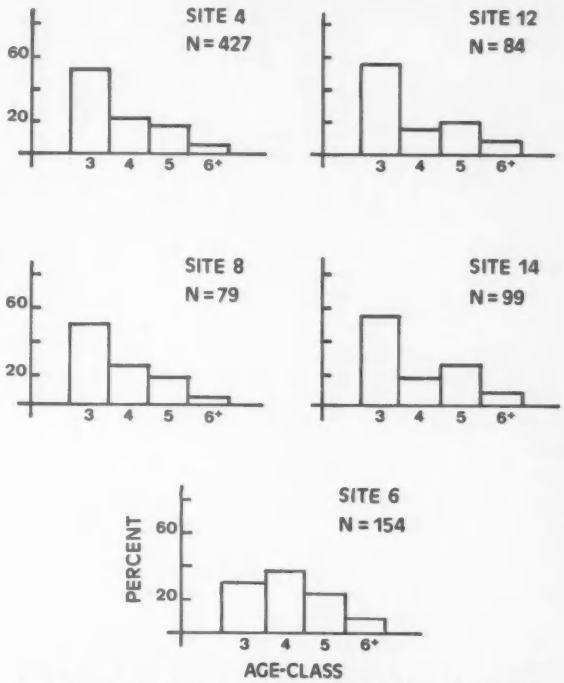


FIG. 3. Proportional histograms of the age distributions of male yellow perch collected from five isolated spawning sites in Lochaber Lake, N.S., June 6–26, 1984.

As noted above, mature female Lochaber perch consistently prefer to spawn at certain sites and use others sparingly. Our first model assumes that spawning sites are randomly selected by perch each year. Additionally we assume that the probability that perch will select a spawning site depends only on the physical or chemical characteristics of a particular site which are relevant to spawning, e.g. bottom composition, slope (Newsome and Aalto 1987; Dorr 1982), or other attractive or aversive features. Therefore, the assumption that selection of a spawning site is random each year means that the number utilizing a given spawning site will be proportional to the probability that this site will be utilized times the total number spawning that year. This model predicts that year and spawning site will be independent and further that the age distribution will be the same at each site. We can reject this model on the basis of the tests of independence regarding annual distributions of egg-masses reported above, as well as the fact that our evidence shows that there are at least two, and possibly more, distinct age distributions.

Our second model assumes that only first-time spawners select spawning sites randomly, while repeat spawners utilize the site where they initially spawned. This model is based on that model hypothesised for walleye (*Stizostedion vitreum vitreum*) (Colby and Nepszy 1981; Horrall 1981; MacLean and

Evans 1981). As above, the initial selection of a spawning site and year are assumed to be independent. This model apparently permits populations to behave independently of one another, since survival rates may be age and site specific, but additional considerations suggest that this model can also be rejected on the basis of the evidence presented above.

Newsome and Aalto (1987) observed that the survival rate for perch from embryo to age 3 does vary by a factor of nearly 10. Clady (1976) noted that the survival rate from embryo to a pelagic stage, 3 or 4 wk later, varies by a factor greater than 10. Others (Nakashima and Leggett 1975; Craig et al. 1979; Aalto and Newsome 1980) noted that age-specific survival rates for older perch tend to be constant over time. The greatest variation in the survival rates for yellow perch occurs during the first summer. The age-specific survival rates are more or less constant after the perch become mature at age 3.

These observations suggest that the groups of perch utilizing different spawning sites should exhibit similar age structures, since each year the proportion of first-time spawners utilizing a spawning site will be determined by the time-independent probability that a perch will select that spawning site, and subsequently, the perch utilizing a given spawning site experience very similar age-specific survival rates. These considerations and the fact that first-time spawning females constitute approximately 50% of the Lochaber Lake spawning population (Newsome and Aalto 1987) suggest that the year-to-year variation in the number of female perch utilizing various spawning sites would be approximately synchronous. Thus, although this model apparently permits local populations which could vary independently, these additional observations suggest that the observed behavior of this model would be very similar to the first model discussed above, and therefore we can reject it.

The third model we propose is the demic model. Since each perch spawns at the spawning site where it hatched, local populations defined by spawning sites can reflect local variations in survival rates of young-of-the-year (YOY). Thus the demic model is consistent with the results reported above.

Phenomena that would produce differential survival rates for YOY at different sites are described in Newsome and Aalto (1987). Briefly, variations in mortality of embryonic perch and perch fry are related to annual variations in the amount of thermal shocking during the developmental period. Thermal shocking arises as a result of wind-driven seiches (we have observed changes of 7°C within a period of 15 min at a depth of 10 m during the spawning season). Since the pattern of winds can be different in different years, and because the topography of the lake bottom varies at different sites, each site may undergo a different thermal regimen during each spawning season; e.g. downwind spawning sites will be warmer at a given depth due to surface waters, while upwind sites will be cooler due to upwelling water. Thus the survival rates of embryonic perch and perch fry can vary widely from site to site.

Two behaviors that may be involved in the demic structure of the Lochaber perch population are that first-time spawners would follow experienced spawners to their common natal site, and schooling behavior. Stabell (1987) has made a careful study of the ability of atlantic salmon (*Salmo salar*) parr to cue on pheromones. Horrall (1981) suggested that this ability may be common among fishes. Thus the mechanism suggested for the first of these behaviors is that first-time spawners follow pheromone trails left by older spawners. This behavior would be facilitated by the schooling behavior exhibited by yellow perch. Perch form schools which are stratified by size and/or age (Scott and Crossman 1973; Thorpe 1977; MacLean and Magnuson 1977). We have observed during July and August that Lochaber yellow perch schools are typically composed of perch age 2 or more, or yearling perch. YOY perch are pelagic through most of the summer and return to the littoral zones of lakes during the late summer or early fall. YOY perch are also reported to exhibit schooling behavior (MacLean and Magnuson 1977). The size and/or age stratification of schools is a useful behavior for perch, since they are also known to be cannibalistic (Thorpe 1977; Holcik 1977). Members of a school of older perch would learn their way to their natal spawning site by the pheromone mechanism suggested above, and the first-time spawning perch can then follow the pheromone trails of the older spawners. The evidence we have found regarding the differences in age structure through the spawning season is consistent with these observations.

Although our evidence does not prove that the demic model is the correct model for perch in Lochaber Lake, we have been able to provide strong arguments to reject competing models of perch spawning behavior. Further, our evidence is consistent with the demic model, and we have provided a plausible mechanism which explains our observations.

The results of the Windermere study of perch population dynamics are also supportive of the demic hypothesis. The dynamics of the north and south basins of the lake exhibit asynchrony in annual variations in abundance over a long period of time (Craig et al. 1979). This evidence can only be used to infer that the Windermere demes, providing they exist, are either large or can only be located within large bodies of water. Evidence reported by other authors (Willemsen 1977; Nakashima and Leggett 1975) can also only be used to conclude that demes occupy a portion of a relatively large body of water (e.g. half of a 1200-km$^2$ lake or half of a 40-km-long lake, respectively).

Assuming that the Lochaber perch do exhibit demic behavior, our results permit inferences regarding the separation of demes. The minimum and maximum distances between any two sites in Lochaber Lake are, respectively, 0.4 and 4.5 km. These distances are similar to the commonly reported ranges of movement of yellow perch of 0–4 km reported by various authors (Rodeheffer 1941; Fortin and Magnin 1972; Thorpe 1977) and well within the maximum reported ranges of 27–320 km (Nakashima and Leggett 1975; Dorr 1982). Lochaber Lake has at least two circulations which may divide the lake into two different demes (cf. Fig. 1). The maximum distance between sites 1, 2, 4, 8, 10, and 11 which lie in the southern circulation is 1.7 km. The chi-square scores for the egg-mass counts suggest that only site pairs 2 and 11 and 4 and 10, which lie in the southern circulation, might have similar population dynamics for mature female perch. Site pairs 1 and 4 and 8 and 10, which are separated by distances of 0.4 and 0.5 km, display different population dynamics for mature female perch according to the chi-square scores. This distance is less than the minimum suggested distance between two distinct stocks of lake whitefish (*Coregonus clupeaformis*) in Lake Huron (Ihssen et al. 1981). Ihssen et al. based their suggested minimum distance for sympatric stocks on more parameters than considered here. The inclusion of more parameters would have the effect of maintaining or increasing the distinctions between the perch at different sites (i.e. another parameter would be the same for all sites leading to no further discrimination or would be different for some of the sites leading to further distinctions). The results here suggest that demes could be separated by as little as 0.4–0.5 km of open water.

Although our observations are only indirectly supportive of the demic hypothesis, this evidence, along with the independent conclusions of other perch investigations, suggests that it would be prudent from a management point of view to regard perch populations as demically structured. Further support is provided by the fact that the closest percid relative of the perch, genus *Steizostedion* (walleye and sauger), is known to exhibit this behavior (Scott and Crossman 1973; Spangler et al. 1977). Direct evidence will be difficult to obtain, requiring a large expenditure of time and effort. The use of genetic markers, used to confirm demic structure among walleye and sauger populations, or tetracycline marking may be useful in the future to clearly demonstrate this phenomenon. However, even if such studies were begun immediately, confirmatory results would not be available until, at best, 1991.

The possibility of demic structure in populations and the possibility that size of these demes could be small suggest that great care must be taken in studying such populations. Sampling the population at one or a few sites may lead to large errors if the sampled sites are unrepresentative of the variation among the different demes in the body of water defining the population under study.

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# Matrix Analysis of Co-occurrences of Fishes of the Scotian Shelf and Bay of Fundy

J. S. Scott

*Department of Fisheries and Oceans, Marine Fish Division, Biological Station, St. Andrews, N.B. E0G 2X0*

Scott, J. S. 1989. Matrix analysis of co-occurrences of fishes of the Scotian Shelf and Bay of Fundy. Can. J. Fish. Aquat. Sci. 46: 191–197.

Numbers of co-occurrences of 29 common fishes of the Bay of Fundy and Scotian Shelf were derived from annual research trawl survey data for the summers of 1970–79 and the spring, summer, and autumn seasons of 1980–84. Matrices prepared from the data were used to examine degrees of association between different species and seasonal and geographical variation in the associations. Three categories of associations were identified: shallow water with a dominant winter flounder (or yellowtail flounder) – longhorn sculpin – sea raven assemblage; middepth with a dominant cod – haddock – thorny skate assemblage; deepwater characteristic species but with no strong recurring assemblages. Strength of co-occurrence was directly related to species abundance and changes corresponded to known seasonal movements in several species, including silver hake, spiny dogfish, and pollock. In general, the strength and number of co-occurrences decreased from southwest to northeast along the Scotian Shelf. The Bay of Fundy was exceptional, with strong co-occurrences of shallow-water species and poor representation of deepwater fishes.

On a déterminé le nombre de co-occurrences réunissant certaines des 29 espèces communes de la Baie de Fundy et de la plate-forme Scotian d'après les résultats des relevés de recherche annuels effectués au chalut en été, de 1977–79, ainsi qu'au printemps, en été et en automne, de 1980 à 1984. On a utilisé ces données pour élaborer des matrices devant servir à évaluer le degré d'association entre les différentes espèces considérées et les variations saisonnières et géographiques des associations. On a trouvé trois types d'associations : une association en eau peu profonde, dominée par la plie rouge ou par un groupement réunissant la limande à queue jaune, le chaboisseau à dix-huit épines et l'hémitriptère atlantique; une association de profondeur médiane, dominée par un groupement réunissant la morue, l'aiglefin et la raie épineuse; enfin, des espèces caractéristiques des eaux profondes, mais sans formation répétée de groupements bien établis. On a constaté que l'importance des co-occurrences est directement liée à l'abondance des espèces et que les changements observés correspondent aux mouvements saisonniers de plusieurs espèces, notamment le merlu argenté, l'aiguillat commun et la goberge. On a aussi noté qu'en général, le nombre et l'importance des co-occurrences diminuent du sud-ouest au nord-ouest le long de la plate-forme Scotian. La Baie de Fundy était exceptionnelle : on a noté d'importantes co-occurrences réunissant des espèces des eaux peu profondes, tandis que les espèces des eaux profondes étaient pauvrement représentées.

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Analytical studies of groupings of marine fishes, under the terms "species composition," "fish assemblages," "species interaction," etc., have used statistical tests ranging from the comparatively simple (Fager and Longhurst 1968) to complex (Colcoveresses and Musik 1984; Mahon et al. 1984). The aims have ranged from contributing to our knowledge of factors determining fish distributions and associations (Foger and Longhurst 1968) to providing a basis for management of multispecies fisheries (Gabriel and Tyler 1980; Mahon et al. 1984). Most of the studies were conducted on areas of the continental shelves where the bottom sloped fairly evenly to the shelf edge, and they related the derived species assemblages to a progressive and orderly change in depth, with bottom type as a minor determinant. The one exception is that of Mahon et al. (1984). They studied the Scotian Shelf and Bay of Fundy, where the bottom topography is variable, ranging from as little as 20 fathoms (36 m) on some of the banks to more than 120 fathoms (218 m) in basins, canyons, and channels (Fig. 1), with an equally complicated surficial geology (King 1970; MacLean and King 1971; Drapeau and King 1972; Fader et al. 1977) which also affects fish distribution (Scott 1982a).

The sophisticated cluster analysis techniques and site selection used by Mahon et al. (1984), incorporating temperature, bottom type, and salinity as factors, tended to obscure purely geographic differences in fish assemblages, the viewpoint taken in the present treatment, although geographic area was used as a factor in considering species composition in relation to site type. This is not to imply that geographic features are the most fundamental factors contributing to species associations, but they are a convenient basis for examination of the Scotian Shelf where the Northwest Atlantic Fisheries Organization (NAFO) divisions and subdivisions are also ecological entities with individual characteristics as exhibited by fish stocks, topography, and oceanographic regimes.

In an attempt to identify geographic differences and possibly related seasonal changes in species associations of individual species, the technique of comparing the patterns revealed in

matrices of co-occurrence of species is used here for the same area and with the same data as Mahon et al. (1984), with the addition of seasonal data. The clustering techniques used by Mahon et al. (1984) do not permit examination of individual species to the same degree.

## Materials and Methods

Details of data collection are given in Mahon et al. (1984). The results of 3316 trawl sets, comprising 1194 in the 1970–79 summer series and 688, 665, and 769 in spring, summer, and autumn, respectively, of the 1980–84 series, were used in the study. The sets were made according to a depth-stratified random sampling design (Halliday and Koeller 1981). Each set consisted of a standard 0.5-h tow with a bottom trawl, No. 41 Yankee, or Western IIA, fitted with a fine-mesh codend liner. Catches were sorted by species and details of position, depth, etc., recorded for each set, together with numbers, weights, and other biological observations on the fishes. The majority of fishes captured were adults, but at certain seasons, considerable numbers of juvenile cod, haddock, and silver hake, in particular, were taken. No distinction is made here between adults and juveniles. A selection of 29 fish species was made: those that occurred frequently in survey trawl catches, or were significant as prey species (sand lance), or were known to be abundant but poorly sampled by bottom trawl (herring, mackerel). One important species, red hake, is not included because in the early years of the surveys there was a convention that the species, prevalent to the south of Browns Bank (Fig. 1), was replaced by white hake from Browns Bank to the north and northeast. In later years, the two species were distinguished but, for the present study, the two species are combined as white hake.

Matrices were constructed to show the number of times which each species occurred with every other species. This was done for each of the areas (Bay of Fundy, southwest Shelf (NAFO Division 4X excluding Bay of Fundy); central Shelf (NAFO Division 4W); northeast Shelf (NAFO Subdivision 4Vs) (Fig. 1)) and for the seasons (spring (March), summer (July), autumn (September–October)). Sydney Bight (NAFO Subdivision 4Vn) was omitted because of the relatively low number of sets made there. The numbers of co-occurrences were then standardized on the basis of 100 tows per category; the numbers of tows ranged from 78 in the Bay of Fundy in summer to 445 in Division 4W, also in summer, with approximately the same density of stations in each area.

Comparison of matrices was made by subjective examination. The order of listing of species is a potentially critical factor in revealing species groupings by use of matrices. A number of alternatives are available, including results of cluster analysis (Colcoveresses and Musik 1984), temperature, depth, salinity, and bottom type preferences (Mahon et al. 1984), and systematic relationships (Family or Order). Depth and bottom type tend to be correlated on the Scotian Shelf (Scott 1982a) and were identified as major determinants of species association in previous studies (Fager and Longhurst 1968; Mahon et al. 1984). Comparison was made of the effects of order of listing by depth preference (Scott 1982b), bottom type preference (Scott 1982a), systematic group, and cluster analysis (Mahon et al. 1984) in order to select the best resolution of groups of co-occurrent species. The criteria for "best resolution" were clarity of group definition and degree of clustering along the diagonals of the matrices. On that basis, depth preference was

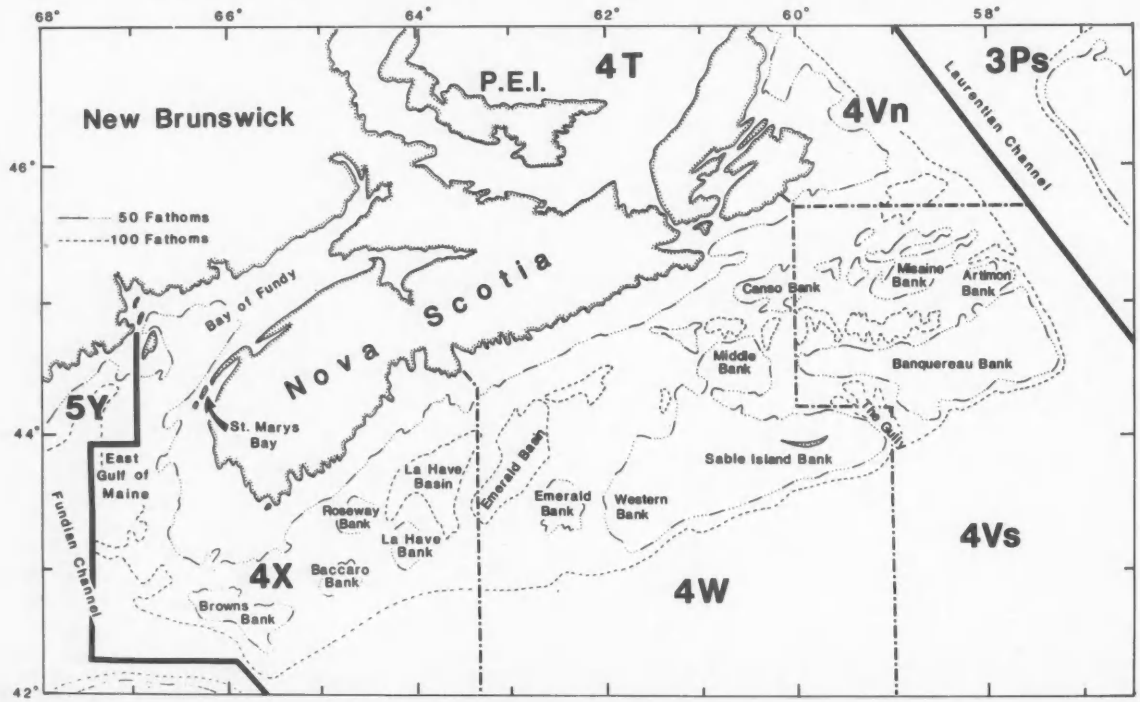


FIG. 1. Bay of Fundy and Scotian Shelf with NAFO divisions.

selected as the standard order of species. The preferred depth was that at which the weighted mean catch per tow (kilograms) was greatest for each species. It corresponded well to the depth range over which >10% of the catch for each species was made. The species order by depth was similar to the order arrived at by Mahon et al. (1984) using their various techniques.

The terms "strong," "moderate," and "weak" are used to describe degrees of co-occurrence in the 50–100, 25–49, and 0–24% categories, respectively.

Matrices for the summers of 1970–79 and 1980–84 (Scott 1987) showed that there was little change between the two periods in patterns of species grouping. The most evident difference was that, in general, co-occurrences were stronger in 1980–84 but the actual relationships between species were similar for corresponding areas. The 1980–84 series may be taken, therefore, as representative of the situation over the period since 1970.

## Results

Cursory examination of the matrices shows three major groupings of fishes: shallow water, middepth, and deep water, fortuitously separated in the diagrams by species with low degrees of association. The middepth cod – haddock – thorny skate group was dominant in all areas. It was extremely strong in the Bay of Fundy (Fig. 2A), but diminished progressively from southwest to northeast (Fig. 2B–2D) where haddock, in particular, was rather poorly represented. This pattern of weakening degree of association to the northeast applied to all the matrices but was especially true of the shallow-water group (Table 1).

The Bay of Fundy was quite distinct from other areas. The shallow-water species winter flounder, longhorn sculpin, and sea raven were strongly associated with most other species of shallow and middepths, but yellowtail flounder and winter skate, common in other areas, were weakly associated or absent. In contrast with most of the shallow-water group, the deepwater species longfin hake, argentine, grenadier, and eelpout were virtually absent from associations in the Bay although redfish co-occurred with several species.

The major statistical divisions and subdivisions of the Scotian Shelf, 4X, 4W, and 4Vs, had many features in common, with rather similar species groupings and emphasis on middepth species. Variation in strength of co-occurrence appeared as a southwest to northeast trend (Fig. 2B–2D).

Detailed examination of the matrices shows that the fishes may be divided into three categories:

(1) Species with low to moderate degrees of co-occurrence but which appear to be adequately represented in the catches. These may be subdivided into (a) solitary species which occur comparatively infrequently and in low numbers in catches (angler, eelpout, halibut, ocean pout, wolffish); cusk is also included in this subcategory but its low representation may be due to its preference for rocky habitat (Leim and Scott 1966) not adequately sampled by the trawl; (b) fishes of deep water where species diversity is low (argentine, grenadier, longfin hake); and (c) fishes which are locally abundant but which do not associate closely with other species (little skate, smooth skate, winter skate).

(2) Species which are not adequately represented in the catches (herring, mackerel, sand lance). Herring and mackerel are at least seasonally abundant but are largely unavailable to the bottom trawl because of their pelagic habit. Sand lance are locally abundant (Leim and Scott 1966) but are elusive because of their small size and feeding and burrowing behavior.

(3) Species assumed to be adequately represented in catches.

## Discussion

The resolution of the fishes listed in the matrices by depth preference into fairly well-defined groups indicates that depth, or a correlated factor, such as temperature or bottom type, is important in determining species associations. The strengths of the associations, however, are evidently determined largely by species abundance. Comparison of a list of species in order of abundance with a list in order of an index of co-occurrence based on the matrices showed strong correspondence (Scott 1987).

The cod – haddock – thorny skate association is the dominant grouping in the area surveyed. The high degrees of co-occurrence of these species do not necessarily imply an affinity between them, however. Cod and haddock are systematically related but their feeding (Langton and Bowman 1980), spawning behavior, and geographic distribution (Scott 1976) differ to a considerable extent. Thorny skate is far removed systematically from the others, with radically different feeding habits and behavior. Similarly, the individual species of the other outstanding association, the shallow-water winter flounder (or yellowtail flounder) – longhorn sculpin – sea raven group, show major differences in systematics, feeding, and behavior (Scott 1976). There are no obvious benefits to be gained from the associations and they would seem to be fortuitous within the constraints of similar environmental or food preferences. The one exception appears to be the cod–haddock association. This is strong wherever the two species are abundant and the association is closer than would be expected from two species with similar depth preference (Scott 1982b), but different food and bottom-type preferences (Langton and Bowman 1980; Scott 1982a). The close association extends even to juveniles which are quite frequently captured together (personal observation) and have been observed together in mixed schools.

Close associations of different species do occur in nature but they are predator–prey relationships (e.g. cod and sand lance), symbiotic (e.g. pilot fish, shark sucker), commensal (e.g. cichlids (Jackson et al. 1963)), or environmental (e.g. cod – haddock – thorny skate) rather than affinities. Some associations are exceptionally close but may be temporary and subject to rapid change (Watt 1987).

Seasonal influences play a part in determining co-occurrences. A problem here is in identifying the species which governs the seasonal change in associations. The change is relative and dependent on one species showing consistent variation in co-occurrence in relation to other species which are otherwise comparatively stable. Determination is aided by what is known of seasonal movements of fishes in the area concerned and examining the reciprocal relationships between the species in catches, e.g. cod may appear in a great majority of catches in which winter flounder is present, but winter flounder in only a small minority of catches in which cod appears.

Several species, including silver hake, spiny dogfish, white hake, pollock, haddock, and herring, show well-defined seasonal changes in co-occurrences.

Silver hake co-occurrence strengthened consistently from spring to autumn with a concurrent increase in associations with shallow-water fishes in summer in 4W and in autumn in 4W and 4X and with middepth and deepwater fishes in autumn.

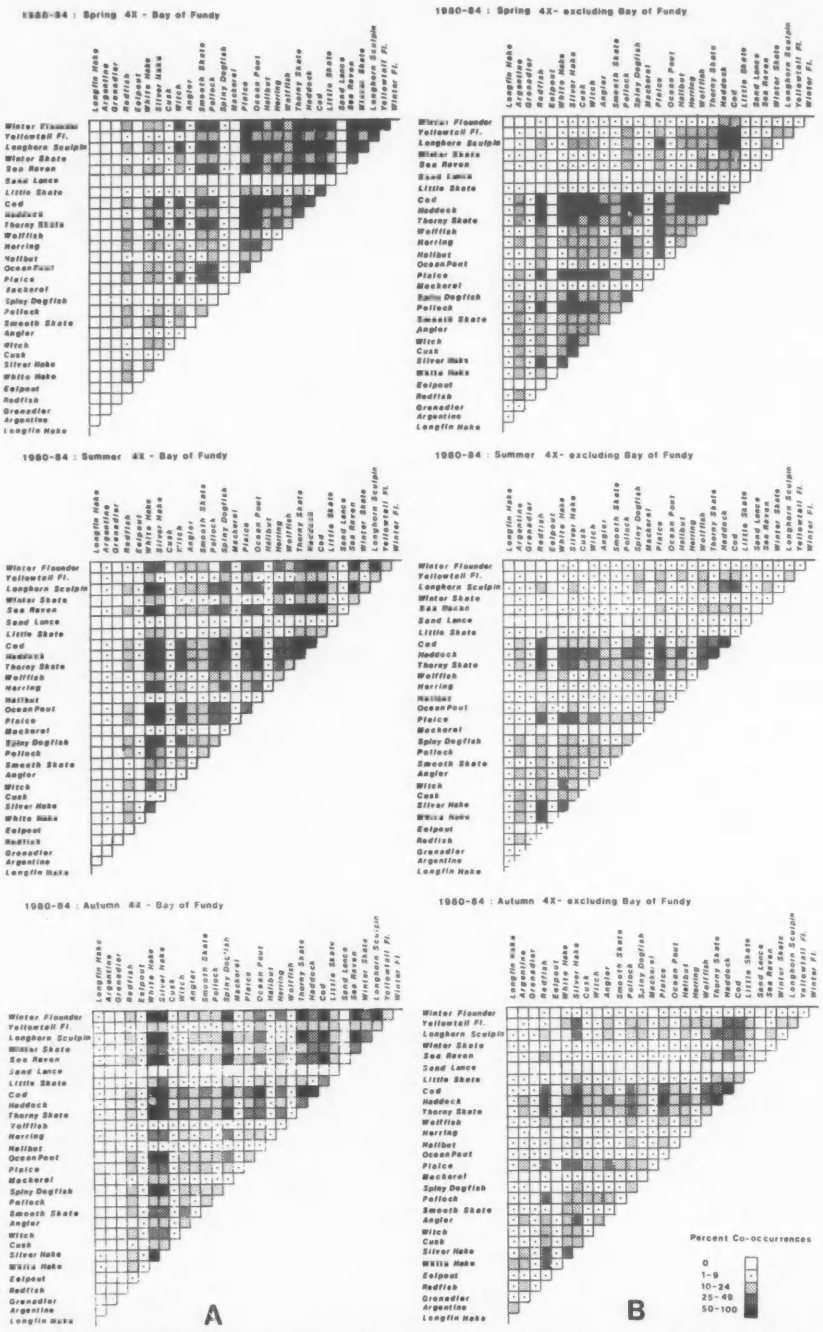


FIG. 2. Matrices of percent co-occurrences of fishes from research trawl surveys of the Bay of Fundy and Scotian Shelf, 1980–84, by NAFO division and season. (A) Bay of Fundy; (B) 4X excluding Bay of Fundy; (C) 4W; (D) 4Vs. (Figure 2 concluded next page)

The changes correspond to the migration of silver hake from deeper water of the Shelf slope and the basins to the shallower water on the banks where they spawn in summer and early autumn before going deeper again in winter.

Associations with spiny dogfish were concentrated in the southwest part of the Shelf and Bay of Fundy. In the latter area, co-occurrences intensified from spring to autumn, but in 4X they peaked in summer. The pattern follows the movement of

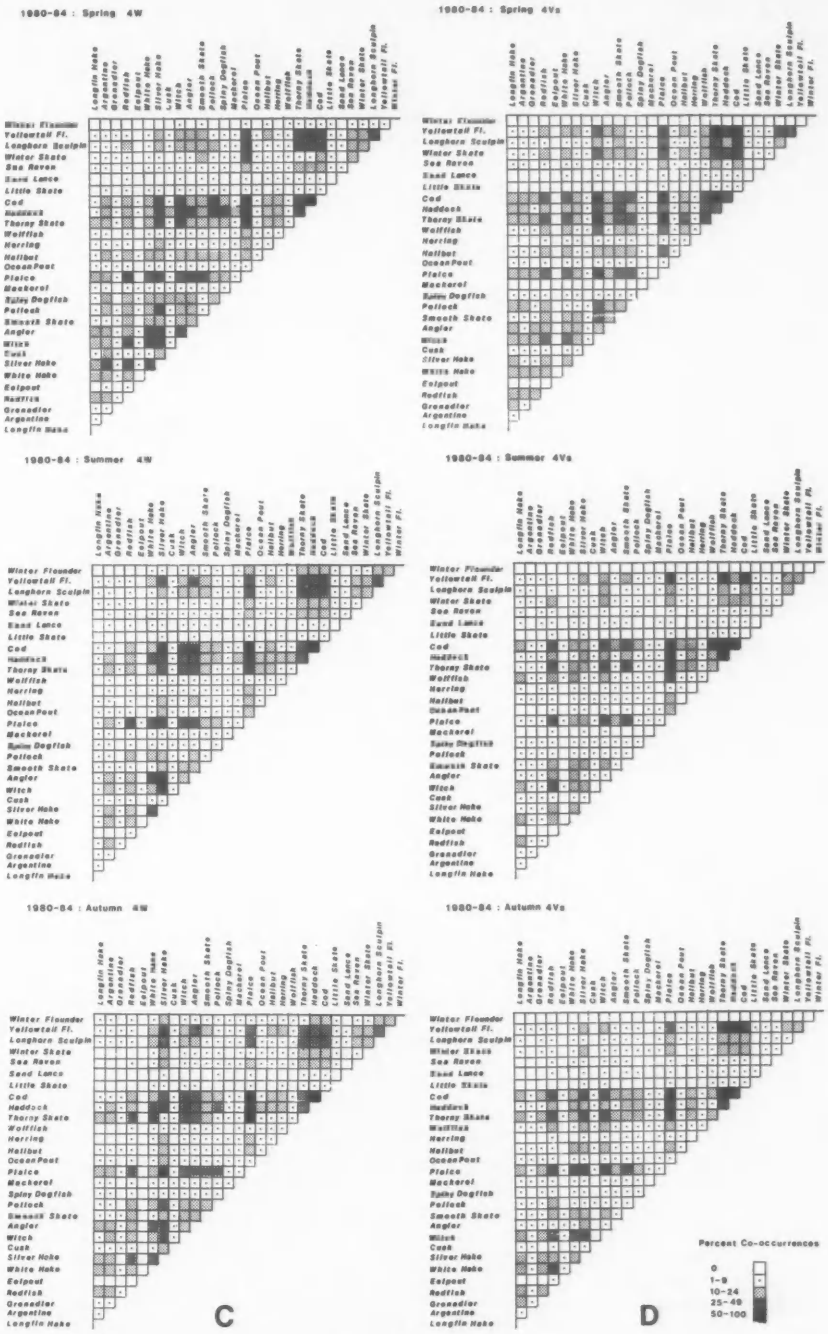


FIG. 2. (Concluded)

dogfish from the southwest and deeper water into the Bay and onto the Shelf in spring and the progressive withdrawal in late summer and autumn to overwintering areas.

White hake showed considerable seasonal variation in co-occurrences but it is difficult to determine whether the changes are the result of movements of the fish or of its associates. The pattern of strengthening co-occurrences from spring to autumn in the Bay of Fundy corresponded to a weakening in 4X. This may indicate seasonal movement of white hake from 4X into the Bay of Fundy through the year with a return to 4X in winter.

In contrast with the above species, pollock had its strongest associations in spring, with diminishing levels through summer

TABLE 1. Species showing strong co-occurrence with other fishes of the Bay of Fundy and Scotian Shelf, by NAFO division and season. Sp = spring; Sum = summer; Aut = autumn.

| | Bay of Fundy | | | 4X | | | 4W | | | 4Vs | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sp | Sum | Aut | Sp | Sum | Aut | Sp | Sum | Aut | Sp | Sum | Aut |
| Winter flounder | + | + | + | | | | | | | | | |
| Yellowtail flounder | | | | + | | | | | | + | | |
| Longhorn sculpin | + | + | + | + | | | | | | | | |
| Sea raven | + | + | + | | | | | | | | | |
| Cod | + | + | + | + | + | + | + | + | + | + | + | + |
| Haddock | | + | | + | + | + | + | + | + | | | |
| Thorny skate | + | | | + | + | + | + | | + | + | + | + |
| Herring | + | | | | | | | | | | | |
| Ocean pout | + | | | | | | | | | | | |
| Plaice | + | | | + | + | + | + | + | + | + | + | + |
| Spiny dogfish | | + | + | | | | | | | | | |
| Pollock | | | | + | | | | | | | | |
| Witch flounder | | | | | | | | | | + | + | + |
| Silver hake | | | + | | | | | | + | | | |
| White hake | | + | + | | | | | | + | | | |

to autumn in the Bay of Fundy and 4X, but summer minima on the central and northeast parts of the Shelf. The comparatively strong spring co-occurrences in the southwest correspond to early spring movements of pollock from the Gulf of Maine to the Bay of Fundy and the Scotian Shelf. The higher spring levels in 4W, 4Vs, and 4Vn may originate as part of the same influx but the higher autumn levels in those areas are inexplicable unless they are due to movements of the pollock stock of the central Shelf (McGlade 1983). Another possibility is that the higher autumn level is due to seasonal movements of cod, haddock, and silver hake rather than pollock.

Haddock co-occurrences were exceptional in the Bay of Fundy in that they strengthened from spring to summer and then weakened in autumn. The reciprocal pattern appeared in 4X, but to a less marked degree, suggesting that there is a summer migration of haddock from the southwest Shelf into the Bay. The weakening associations of haddock towards the northeastern part of the Shelf corresponds to the distribution of these fish over the Shelf. Mahon et al. (1984) suggested that there might be a special predator–prey relationship between halibut and haddock but there is no evidence of that in the matrices.

Herring, although a pelagic species and generally unavailable to the bottom trawl, was comparatively well represented in associations, particularly in the Bay of Fundy but also in 4X and 4W. Co-occurrences were stronger in spring than in other seasons, which would be expected in relation to known overwintering in 4W. It may also be due to increased availability to the bottom trawl as a result of the herring moving offshore into deeper water near bottom in winter or to offshore migration to summer spawning areas. The association of herring with catches of middepth and deepwater fishes in 4X and 4W supports the latter possibilities. The association is presumably accidental or a predator–prey relationship because, outside spawning periods when herring select specific sites, the pelagic and semipelagic fishes herring, mackerel, and pollock are not closely related to the bottom.

The characteristics of co-occurrences in the Bay of Fundy were quite distinct from those of all other areas. Associations were generally stronger, with the shallow-water fauna well represented, but redfish is the only significant representative of deepwater fishes. There were strong co-occurrences between many middepth and shallow-water species, which suggests that depth was a less important factor in determining associations than in other areas. Seasonal variations were also emphasized in the Bay, with changes in silver hake, white hake, spiny dogfish, pollock, and herring particularly evident. It appears that strong tidal mixing of the waters of the Bay, together with unusually high concentrations of middepth and shallow-water species, leads to a more uniform environment and higher degree of mixing of fishes than is found in the more thermally structured and topographically varied environment of the open Shelf. It is possible that a factor such as availability of food overrides the other factors which are effective on the Shelf in determining concurrences.

The areas of the main part of the Scotian Shelf, from 4X to 4Vs, showed rather similar characteristics of co-occurrences of the fishes. The changes between areas were in the nature of a decreasing southwest to northeast trend in strength of association, corresponding to changes in distribution of species (Scott 1976). The major exceptions were the deepwater witch flounder, grenadier, and longfin hake and the shallow-water yellowtail flounder and winter skate, in which associations strengthened. Cod, thorny skate, and plaice, the species with strongest associations, showed little change between areas in accordance with their rather uniform geographic distributions (Scott 1976). The southwest to northeast trend in co-occurrence corresponds to a decreasing trend in bottom temperature (Scott 1982b), suggesting that temperature is a factor in determining the distribution, abundance, and associations of the fishes. Yellowtail flounder was the characteristic flatfish of the shallow-water group, replacing winter flounder which predominated in the Bay of Fundy. The evident lack of association between these two flatfishes may be related to preferences for bottom type. Winter flounder is generally associated with coastal waters on mud or hard bottom (Leim and Scott 1966) and is common in the littoral zone in all areas in summer. Yellowtail flounder is typically an offshore species on clean sand bottom (Leim and Scott 1966; Scott 1982a). The rough nature of the bottom in the coastal waters of the Scotian Shelf precludes the standard bottom trawling so that winter flounder is probably underrepresented in the survey data.

A weakness in estimating species associations over extensive areas at sea lies in the sampling methodology. In the present work, the standard trawl tow was for 30 min at 3.5 knots. This

covers about 1.75 naut mi (3.2 km). Depth, bottom temperature, and bottom type may not vary greatly, as tows are generally along depth contours in limited depth zones (0–49, 50–100, 100+ fathoms), so catches will usually comprise species with similar environmental preferences. The tows could sample widely separated groups of different species, however, and this is occasionally evidenced in large catches as stratification of species in the codend (personal observation).

Co-occurrence data have obvious applications in predicting expected composition of fish catches in given areas at given times. A difficulty with using the present results in the fisheries lies in the fact that the research surveys are based on random distribution of fishing stations, stratified by depth, whereas commercial fishing operations are usually directed at selected species of good market value. Fishing skippers tend to limit their operations to specific localities and seasons in which experience has shown that good catches can be expected. The co-occurence data should certainly indicate the proportions of species strongly associated with, say, cod which would be taken in a commercial fishing set in a given area and season, but might not be so effective for weaker associates.

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# A Method for Estimating Uptake and Production Rates for Urea in Seawater using [$^{14}$C] Urea and [$^{15}$N]Urea[1]

Dennis A. Hansell and John J. Goering

*Institute of Marine Science, School of Fisheries and Ocean Sciences, University of Alaska - Fairbanks, Fairbanks, AK 99775-1080, USA*

Hansell, D. A., and J. J. Goering. 1989. A method for estimating uptake and production rates for urea in seawater using [$^{14}$N]urea and [$^{15}$C]urea. Can. J. Fish. Aquat. Sci. 46: 198–202.

Improved estimates of the rates of urea production and uptake by natural populations of phytoplankton were made after determining the change in $^{15}$N-atom % enrichment of urea during incubations. A [$^{14}$C]urea method is described by which the change in enrichment is measured. Estimates of uptake rates are increased (relative to uptake rates determined without correction for isotope dilution) by up to 83% using a $^{15}$N accumulation model and by >210% using a $^{15}$N disappearance model. A discrepancy exists between [$^{15}$N]urea removed from the aqueous phase and $^{15}$N accumulated in the particulate phase at stations occupied in the northeastern Bering Sea. The ability to find in the particulate fraction the $^{15}$N removed from solution as [$^{15}$N]urea was improved by 72% following removal of the >20-μm particulate fraction. This corresponded to only a 4% reduction in the concentration of chlorophyll *a* and a 37% reduction in the concentration of particulate N. Removal of microzooplankton may have improved the efficiency of urea-N retention by phytoplankton.

Des estimations améliorées du taux de production et d'absorption d'urée par des populations phytoplanctoniques naturelles ont été obtenues après détermination de la variation en pourcentage de l'enrichissement en $^{15}$N-atomique de l'urée au cours de périodes d'incubation. Une méthode de [$^{14}$C]urée est décrite qui permet de mesurer cette variation. Les estimations des taux d'absorption sont augmentées (relativement aux taux d'absorption déterminés sans correction pour la dilution isotopique) de 83 % au maximum grâce à un modèle d'accumulation du $^{15}$N, et de plus de 210 % avec un modèle de disparition du $^{15}$N. Il existe un écart entre la $^{15}$N-urée extraite de la phase aqueuse et le $^{15}$N accumulé dans les particules aux stations visitées dans la partie nord-est de la mer de Bering. La capacité de retracer dans des particules le $^{15}$N retiré de solution sous forme de $^{15}$N-urée a été améliorée de 72 % après l'extraction de la fraction des particules supérieures à 20 μm. Cela correspond à une réduction de seulement 4 % dans la concentration de chlorophylle *a* et à une réduction de 37 % dans la concentration de particules *N*. L'extraction du microzooplancton a pu améliorer l'efficacité de la rétention de l'azote contenu dans l'urée par le phytoplancton.

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The nitrogen cycle in the marine environment is still far from being fully understood. Several models have been developed that attempt to describe the pathways of the nitrogen nutrients most important to phytoplankton (i.e. nitrate, ammonium, and urea); however, because of methodological problems, the models have not been thoroughly tested.

Urea is an endproduct of heterotrophic nitrogen metabolism that can be utilized by phytoplankton when excreted into aquatic environments. Previous studies of urea utilization by phytoplankton in marine ecosystems (McCarthy 1972; Harvey and Caperon 1976; Kristiansen 1983; Harrison et al. 1985; Price et al. 1985) have been unable to accurately report the rate of urea-N removal from solution and accumulation into the particulate fraction because of the effects of isotope dilution on rate determinations. Further, there has not been a rigorous determination of the urea production rate (Price et al. 1985) other than for individual organisms (Eppley et al. 1973; Smith and Whitledge 1977), due to an inability to account for isotope dilution of the nutrient tracer ([$^{15}$N]urea) during incubation.

We have developed a method combining [$^{14}$C]urea and [$^{15}$N]urea with isotope dilution methods that provides simultaneous estimates of the rates of urea removal from solution (disappearance uptake rates), urea accumulation into the particulate fraction (accumulation uptake rates), and heterotrophic urea production. This method builds upon the work of others in the areas of aquatic nitrogen uptake and remineralization (Dugdale and Goering 1967; Blackburn 1979; Caperon et al. 1979; Glibert et al. 1982).

Numerous experiments have been performed to determine nitrogen uptake rates. Following the work of Dugdale and Goering (1967), absolute uptake rates (ρ) were calculated from accumulation of $^{15}$N into the particulate fraction:

$$(1) \quad \rho = (\text{atom \% } {}^{15}N_{xs} \cdot PN)/R \cdot t$$

where atom % $^{15}N_{xs}$ = $^{15}$N-atom % in the particulate sample adjusted to atom % excess by subtracting the natural abundance of $^{15}$N (0.365%), PN = particulate nitrogen content of the sample, $R$ is the $^{15}$N-atom % enrichment of the substrate at the beginning of the incubation, and $t$ is the incubation duration. The model assumed a constant $^{15}$N enrichment of the substrate during the incubation.

[1]Contribution No. 707, Institute of Marine Science, University of Alaska - Fairbanks.

Blackburn (1979) and Caperon et al. (1979) developed identical linear differential equation models (here referred to as the Blackburn–Caperon model) for the simultaneous determination of ammonium disappearance and production rates. The Blackburn–Caperon model does not assume a constant value for $^{15}N$ enrichment of the substrate, and thus, the initial and final values must be measured. The production rate ($D$) is calculated as

$$(2)\quad D = \{\ln[(R_t - F)/(R_0 - F)]/\ln(C_t/C_0)\}\cdot[(C_0 - C_t)/t]$$

where $F$ is the natural abundance of $^{15}N$, $C$ is the substrate concentration, and the subscripts 0 and $t$ refer to initial and final values. The disappearance uptake rate ($U$) is calculated as

$$(3)\quad U = [(C_0 - C_t)/t] + D.$$

Glibert et al. (1982) combined the concepts of the Blackburn–Caperon and Dugdale and Goering (1967) models for calculating $NH_4^+$ uptake and production rates. Accumulation uptake rates were calculated after measuring the accumulation of $[^{15}N]NH_4^+$ into the particulate fraction and the changes in $^{15}N$ enrichment of the $NH_4^+$. Laws (1985) presented a formula for calculating accumulation uptake rates ($P$) that requires determination of the Blackburn–Caperon disappearance uptake rate ($U$):

$$(4)\quad P = U\cdot(\text{atom \% } {}^{15}N_{xs}\cdot\text{PN})/(C_0R_0 - C_tR_t).$$

Dual-Label Model

The Blackburn–Caperon and Laws (1985) equations have not been used for estimating rates of urea uptake and production because $R$, the $^{15}N$-atom % enrichment of urea, could not be measured. This problem has been overcome by inoculation of samples with both [$^{15}N$]urea and [$^{14}C$]urea. The [$^{15}N$]urea is used in the traditional sense to determine the $^{15}N$-atom % excess in the particulate fraction. Because the [$^{14}C$]urea in solution is removed at the same rate as the [$^{15}N$]urea (assuming that isotopic discrimination is negligible), its activity provides a measure of the quantity of [$^{15}N$]urea remaining in solution. Determination of the fractional change in [$^{14}C$]urea enrichment during the incubation provides a measure of the fractional change in $^{15}N$-atom % enrichment.

Enrichment of [$^{14}C$]urea in water is calculated as

$$(5)\quad E = A/(V\cdot SA\cdot C)$$

where $E$ is the [$^{14}C$]urea enrichment, $A$ is the activity of the counted sample, $V$ is the volume of the counted sample, SA is the specific activity of the radiolabeled urea, and $C$ is the concentration of urea. From the enrichment of [$^{14}C$]urea, determined at times $T_0$ and $T_t$, the fractional change ($H$) in enrichment is calculated as

$$(6)\quad H = (E_0 - E_t)/E_0$$

where $E_0$ and $E_t$ are the initial and final enrichments.

The initial [$^{15}N$]urea enrichment ($R_0$) is calculated from the concentration of urea ($C_0$) determined after the addition of [$^{15}N$]urea. Thus, $C_0$ is the sum of ambient and added urea. By calculating $R_0$ in this way, we have negated the effect of a change in the concentration of urea on the enrichment that may occur in the incubation bottles during the period between the recovery of the water from the collection bottles and the addition of nutrients. Hence:

$$(7)\quad R_0 = [S + [(C_0 - S)\cdot 0.00365]/C_0]\cdot 100$$

where $S$ is the concentration of [$^{15}N$]urea in the incubation bottle at the start of the incubation. The final enrichment of [$^{15}N$]urea ($R_t$) is calculated as

$$(8)\quad R_t = R_0(1 - H).$$

Accumulation uptake rates corrected for isotope dilution ($P$) are calculated according to Equation 4. The urea production rate ($D$) and disappearance uptake rate ($U$) are calculated from the Blackburn–Caperon model using Equations 2 and 3, respectively.

## Methods

At two stations in the northeastern Bering Sea, water was collected from the depth of penetration of 50% of the incident photosynthetically active radiation as determined with a Licor LI-185 deck unit and a LI-192S underwater sensor. The water was prefiltered through a 333-μm Nitex screen into three 2.27-L polycarbonate bottles screened with a neutral density filter (Perforated Products, Inc., nickel screens) to simulate the in situ light intensity. Within an hour of sampling the concentration of urea was determined by an automated diacetyl monoxime method (Whitledge et al. 1981), after which 99 atom % [$^{15}N$]urea (Icon Services, Inc.) was added to each of the samples. The final $^{15}N$-atom % enrichment of urea in each sample was less than 5%. In addition, approximately $27 \times 10^{-3}$ μg-at urea-N labeled with $^{14}C$ (1.054 MBq·μg-at urea-$N^{-1}$; New England Nuclear Research Products) was added to each of the samples. After mixing, a 125-mL aliquot was removed from each bottle and the remainder was incubated on deck in Plexiglas incubators cooled with flowing surface seawater.

The 125-mL aliquot was filtered through a 0.6-μm Whatman quartz filter. From the filtrate, triplicate 20-mL aliquots were removed for the determination of the initial concentration of urea ($C_0$). To remove [$^{14}C$]$CO_2$ produced during urea metabolism, the remaining filtrate (50–60 mL) was acidified with 0.5 mL of 1 N HCl and then bubbled with $N_2$ gas for 15 min. Based on experimentation with [$^{14}C$]$HCO_3^-$ in our laboratory, this technique removed more than 99% of the dissolved inorganic carbon from solution. To obtain time-zero activity ($A_0$), 5 mL of the degassed water was added to a scintillation vial containing 15 mL of Scinti Verse I. Counting was performed on a Beckman LS-100C liquid scintillation counter. Twenty-minute counts gave a counting error of 1–1.5%.

Samples were incubated for 6–8 h. Prior to filtration, a 125-mL aliquot was removed and treated as at $T_0$ to determine the concentration of urea ($C_t$) and the activity of [$^{14}C$]urea ($A_t$). The remaining 2.02 L was filtered onto a precombusted (450°C) 0.6-μm quartz filter and rinsed with filtered seawater. The filters were dried at 50°C for 24 h and transported in a desiccator to the laboratory where they were combusted at 800°C for 4 h with approximately 1 g of Cuprox in evacuated and sealed quartz tubes. Particulate nitrogen (PN) was determined from the pressure of $N_2$ measured with an MKS type 122A absolute pressure transducer after breaking the sealed quartz tubes in a high-vacuum manifold connected to an AEI MS20 dual collector mass spectrometer. Isotope ratio analyses were also performed with the mass spectrometer. The coefficient of variation for the ratio of $N_2$ mass to transducer voltage (determination of PN) and the standard deviation for isotope ratio analysis (natural abundance samples) were typically <0.5% and 0.001 atom %, respectively.

TABLE 1. Absolute uptake rates of urea without correction for isotope dilution (ρ) and with correction ($P$ = accumulation uptake rate; $U$ = disappearance uptake rate) and production rates ($D$). Samples are replicated with seawater from the 50% light depth at two stations in the northeastern Bering Sea. $S$ = concentration of [$^{15}$N]urea (exclusive of naturally occurring [$^{15}$N]urea) at the start of the incubation, $C$ = concentration of dissolved urea, $R$ = [$^{15}$N]urea enrichment (%), $A$ = [$^{14}$C]urea activity, $E$ = [$^{14}$C]urea enrichment, $H$ = fractional change in enrichment, and PN = particulate nitrogen concentration. Subscripts 0 and $t$ refer to initial and final incubation times. Units for $S$, $C_0$, $C_t$, and PN are μg-at N·L$^{-1}$, those of $A_0$ and $A_t$ are Bq, and those of ρ, $P$, $U$, and $D$ are μg-at N·L$^{-1}$·h$^{-1}$. Standard deviations are in parentheses.

| Replicate | $S$ | $C_0$ | $R_0$ | $A_0$ | $E_0$ | $C_t$ | $A_t$ | $E_t$ | $H$ | $R_t$ | At% xs | Incubation time (h) | PN | ρ | $P$ | $U$ | $D$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Station 2101 | | | | | | | | | | | | | | | | | |
| 1 | 0.009 | 0.529 (0.115) | 2.060 | 52.540 | 18 846 | 0.389 (0.014) | 25.456 | 12 417 | 0.341 | 1.357 | 0.093 | 6.160 | 2.119 | 0.019 | 0.022 | 0.063 | 0.040 |
| 2 | 0.009 | 0.713 (0.084) | 1.623 | 44.733 | 11 905 | 0.433 (0.123) | 20.054 | 8 788 | 0.262 | 1.198 | 0.100 | 6.160 | 1.969 | 0.025 | 0.025 | 0.082 | 0.037 |
| 3 | 0.009 | 0.473 (0.062) | 2.261 | 50.542 | 20 276 | 0.481 (0.180) | 24.975 | 9 852 | 0.514 | 1.099 | 0.097 | 6.160 | 2.051 | 0.017 | 0.027 | 0.074 | 0.073 |
| | | | | | | | | | | | | | | | $\bar{x}$ = 0.025 (0.002) | $\bar{x}$ = 0.073 (0.009) | $\bar{x}$ = 0.050 (0.020) |
| Station 2120 | | | | | | | | | | | | | | | | | |
| 1 | 0.022 | 0.552 (0.008) | 4.336 | 55.981 | 19 243 | 0.595 (0.012) | 20.165 | 6 431 | 0.666 | 1.448 | 0.608 | 7.500 | 1.725 | 0.035 | 0.067 | 0.098 | 0.104 |
| 2 | 0.022 | 0.508 (0.023) | 4.680 | 51.800 | 19 349 | 0.578 (0.006) | 21.904 | 7 191 | 0.628 | 1.741 | 0.485 | 7.500 | 1.099 | 0.016 | 0.028 | 0.071 | 0.080 |
| 3 | 0.022 | 0.579 (0.005) | 4.151 | 43.475 | 14 248 | 0.633 (0.004) | 15.059 | 4 514 | 0.683 | 1.315 | 0.609 | 7.500 | 1.680 | 0.036 | 0.066 | 0.102 | 0.109 |
| | | | | | | | | | | | | | | | $\bar{x}$ = 0.054 (0.022) | $\bar{x}$ = 0.090 (0.017) | $\bar{x}$ = 0.098 (0.015) |

At an additional station (Station 3093), the particulate phase was size-fractionated to evaluate better the fate of the [$^{15}$N]urea. Prior to incubation, water was passed through 202- or 20-μm Nitex screens or a 3.0-μm Nucleopore polycarbonate membrane. The chlorophyll *a* concentration of each fraction was determined by fluorometry (Strickland and Parsons 1972) using a Turner Designs model 10 fluorometer.

## Results and Discussion

Accumulation uptake rates (Table 1), uncorrected for isotope dilution (ρ), were calculated with $R_0$ (in excess of natural abundance) using Equation 1. Estimates of uptake rates, when corrected for isotope dilution, were increased by averages of 25 and 83% (Stations 2101 and 2120, respectively) with the accumulation model (Equation 4) and by averages of 265 and 210% (Stations 2101 and 2120, respectively) with the disappearance model (Equation 3). The large coefficient of variation (CV) associated with replicate estimates of accumulation rates from Station 2120 (41%) was caused by an anomalously low PN and atom % excess in replicate 2. Replicates 1 and 3 are in very good agreement, with a CV of <0.1%. Station 2101 exhibited a CV of 8% for accumulation uptake rates. Coefficients of variation for urea production rates were 15 and 40% for Stations 2120 and 2101, respectively.

The $^{15}$N data was evaluated for mass balance using $^{14}$C activity in the aqueous phase as an indication of [$^{15}$N]urea remaining in solution. The $^{15}$N that had disappeared from the dissolved [$^{15}$N]urea pool was consistently greater than the amount of $^{15}$N that had accumulated in the particulate fraction (Table 2). On average, 58% (Station 2101) and 37% (Station 2120) of [$^{15}$N]urea removed from solution could not be accounted for in the particulate phase. The missing $^{15}$N may have accumulated as $^{15}$N-labeled dissolved organic nitrogen (DON) or $NH_4^+$. Possible avenues include phytoplankton leakage and grazer-induced losses, such as zooplankton excretion, leakage, and loss of soluble plant material at the mouth parts.

Observations of dissolved inorganic nitrogen disappearance in excess of PN accumulation are not new. Dugdale and Wilkerson (1986) found that 66% of the disappearnce of $NH_4^+$ and 76% of the disappearance of $NO_3^-$ at the 50% light penetration depth off Peru was accounted for by $^{15}$N accumulation in the particulate fraction. Price et al. (1985) reported that the change in concentration of dissolved inorganic nitrogen and urea was consistently greater than the change in PN in frontal waters off British Columbia.

To further evaluate the apparent loss of $^{15}$N from the particulate phase, particulate material was size-fractionated and, following incubation, the resulting $^{15}$N distribution evaluated (Table 2). Although the <20-μm fraction had only a 4% reduction in chlorophyll *a* concentration relative to the <200-μm fraction, there was a 72% improvement in our ability to account for $^{15}$N removed from solution as [$^{15}$N]urea. A 33% reduction in the concentration of chlorophyll *a* (<3-μm fraction) provided no further improvement in the recovery of $^{15}$N. These results point to the importance of the >20-μm fraction in effecting the loss of $^{15}$N. Perhaps large-celled phytoplankton (>20 μm) are especially prone to leak DON and $NH_4^+$, or microzooplankton (>20 μm) play a significant role in causing a grazer-induced loss of nitrogen from the plant cells.

Filtration through the 20-μm screen reduced the concentration of PN by 37%. Much of the PN removed must be detrital; however, a portion also must be composed of microzooplankton

TABLE 2. Fraction of [$^{15}$N]urea removed from the dissolved phase which is unaccounted for in the particulate phase (FR). Stations 2101 and 2120 are replicated at one depth, while Station 3093 is size-fractionated (<200, <20, and <3 μm). $S_0$ and $S_t$ = initial and final concentrations (μg-at N·$L^{-1}$) of [$^{15}$N]urea; $S_t$ is estimated from the fractional reduction in [$^{14}$C]urea activity. Initial ($A_0$) and final ($A_t$) [$^{14}$C]urea activities are expressed in Bq, $[^{15}N]_{xs}$ is the ratio of $^{15}$N to total N in the particulate phase (minus 0.00367), PN is the particulate nitrogen concentration (μg-at N·$L^{-1}$), Chl is the chlorophyll *a* concentration (μg·$L^{-1}$) and FR is calculated as $[(S_0-S_t)-(^{15}N_{xs}\cdot PN)]\cdot[(S_0-S_t)]^{-1}$.

| Replicate | $S_0$ | $(A_0-A_t)\cdot A_0^{-1}$ | $S_t$ | $^{15}N_{xs}$ | PN | $^{15}N_{xs}\cdot PN$ | FR | Chl |
|---|---|---|---|---|---|---|---|---|
| Station 2101 | | | | | | | | |
| 1 | 0.009 | 0.515 | 0.0044 | 0.00093 | 2.119 | 0.00197 | 0.57 | — |
| 2 | 0.009 | 0.552 | 0.0040 | 0.00100 | 1.969 | 0.00197 | 0.61 | — |
| 3 | 0.009 | 0.506 | 0.0044 | 0.00097 | 2.051 | 0.00199 | 0.57 | — |
| Station 2120 | | | | | | | | |
| 1 | 0.022 | 0.640 | 0.0079 | 0.00608 | 1.725 | 0.0105 | 0.25 | — |
| 2 | 0.022 | 0.577 | 0.0093 | 0.00485 | 1.099 | 0.0053 | 0.58 | — |
| 3 | 0.022 | 0.653 | 0.0076 | 0.00609 | 1.680 | 0.0102 | 0.29 | — |
| Station 3093 | | | | | | | | |
| <200 | 0.009 | 0.443 | 0.0050 | 0.00072 | 3.37 | 0.0024 | 0.40 | 3.08 |
| <20 | 0.009 | 0.103 | 0.0081 | 0.00040 | 2.13 | 0.0008 | 0.11 | 2.95 |
| <3 | 0.009 | 0.087 | 0.0082 | 0.00028 | 2.49 | 0.0007 | 0.12 | 2.06 |

and the removal of these grazers improved the nitrogen retention efficiency of the phytoplankton. The removal of the nanoplankton fraction (3–20 μm) provided no further improvement in recovery of $^{15}$N, suggesting that the mechanism controlling the retention of urea-N in the <20-μm size class is common throughout that size class. Possible mechanisms for the apparent loss of $^{15}$N from the <20-μm fraction include grazer-induced and self-induced leakage of $^{15}$N as DON and $NH_4^+$ by the plant cells, analytical errors, and fractionation of [$^{14}$C]urea and [$^{15}$N]urea during uptake (thus providing an error in our estimates of the remaining pool of dissolved [$^{15}$N]urea).

We are confident in our analytical ability to precisely measure the $^{15}$N atom % excess of the PN, the nitrogen content of the PN, and the $^{14}$C activity of the aqueous phase. These measurements, and a knowledge of the initial concentration of [$^{15}$N]urea, provide the only values required for this mass balance analysis. Whereas some fractionation of [$^{14}$C]urea and [$^{15}$N]urea during uptake must exist, we doubt that it could be responsible for the noteworthy lack of accountability of $^{15}$N. This argument is supported by noting the improved accountability of $^{15}$N in the <20-μm fraction, which still contained 96% of the concentration of chlorophyll *a*, over that of the <200-μm fraction.

Plant- and grazer-induced leakage is, then, the most likely cause for loss of $^{15}$N in the <20-μm size class. Plant-induced leakage must account for the bulk of the 11–12% of $^{15}$N removed from the urea pool that could not be accounted for in the <20- and <3-μm particulate phases (Table 2) because there was no improvement in $^{15}$N recovery in the <3-μm size class relative to the <20-μm fraction, while there must have been a reduction in the grazing stress following this fractionation.

In the <200-μm samples, 40% of the $^{15}$N removed from solution as urea could not be accounted for in the particulate pool. If we extend the approximate 10% loss due to plant leakage in the <20-μm fraction to the entire <200-μm plant population, the remaining 30% loss can be attributed to grazing stress. This implies that most of the assimilated urea-N is going into a persistent soluble pool, which only slowly goes to a particulate form. The soluble pool is readily lost during grazing.

Glibert et al. (1985), in discussing the implications of missing $^{15}$N, suggested that it is important to determine whether the uptake of nitrogen by phytoplankton is reported more accurately by the disappearance of $^{15}$N from the dissolved phase or by the accumulation of $^{15}$N in the particulate phase. This is a distinction between gross and net nitrogen uptake by the phytoplankton if we can attribute most of the urea removal to plant cells. Plants probably play the most significant role in urea consumption, since bacterial utilization of urea is not thought to occur at significant rates in oceanic water (Wheeler and Kirchman 1986) and it is unlikely that abiotic pathways for loss of urea are important. As seen here, the difference between the disappearance and accumulation uptake rates can provide insight to the relative importance of plant- and grazer-induced loss of nitrogen.

This method is, in fact, subject to underestimates of the amount of $^{15}$N missing from the combined pool of PN and urea-N. [$^{14}$C]DOC may be released into the water, causing an overestimate of the amount of [$^{15}$N]urea in solution. If this process is important for the autotrophs in the <20-μm fraction, the apparent improvement in accountability of $^{15}$N would be misleading. In other high-latitude waters, <10% of the urea-C taken up by the plants was incorporated into particulate matter, with the rest disposed of as [$^{14}$C]$CO_2$ (Harrison et al. 1985). During our incubations, approximately 50% of the [$^{14}$C]urea was removed from solution. If we assume that 10% of this carbon is incorporated into the organic fraction and that 50% of the assimilated carbon is lost as DOC, then 2.5% of the $^{14}$C initially in solution would be returned as [$^{14}$C]DOC. The [$^{14}$C]DOC returned would cause a 4% underestimate of the amount of $^{15}$N missing from the pool of PN and dissolved urea. Using our data from Station 2101 (replicate 1) and assuming that 2.5% of the urea-C removed from solution is reintroduced as [$^{14}$C]DOC, we calculate that the accumulation and disappearance uptake rates of urea-N would be underestimated by 2.7 and 5.5% and that the production rate of urea-N would be underestimated by 6.3%.

Calculating urea uptake rates based on rates of disappearance provides values that average 140% greater than those calculated for rates of accumulation for northeastern Bering Sea data. Gli-

bert et al. (1982) presented data (their tables 2 and 3) where ammonium disappearance uptake rates exceeded accumulation uptake rates by an average of 197%. The ratio of the rate of urea production to the rate of urea uptake is also greatly affected by the model used for calculation of uptake rates. For Station 2120, the production to uptake ratios are 1.8 and 1.1, respectively, for the accumulation and disappearance models.

Our results show that the in situ production of urea is approximately equal to the consumption of urea (i.e. dynamic steady state) and that a portion of the urea-N that is consumed must be remineralized quickly. Our data suggest that to describe more completely the cycling of urea-N, models must include a dissolved organic pool, as has been recognized for $NH_4^+$ (LaRoche and Harrison 1987).

Prior studies of the uptake of urea by phytoplankton have not accounted for isotope dilution during incubation. Studies of urea regeneration have been limited in the same way and have depended on mass balances and determinations of uptake rates uncorrected for isotope dilution. Our method provides improved and direct estimates of in situ urea production and uptake rates. Trace addition of labeled substrate is achievable with this method, and as a consequence, changes in substrate concentration and fluxes are not significant. The method is performed with relative ease in fresh or marine water and requires minimal effort beyond that needed for conventional uptake experiments which do not account for isotope dilution.

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# Differences in Brown Trout (*Salmo trutta*) Production among Contiguous Sections of an Entire Stream[1]

Raymond M. Newman and Thomas F. Waters

*Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108, USA*

Newman, R. M., and T. F. Waters. 1989. Differences in brown trout (*Salmo trutta*) production among contiguous sections of an entire stream. Can. J. Fish. Aquat. Sci. 46: 203–213.

Production dynamics of a wild brown trout (*Salmo trutta*) population were examined for 3 yr in each of eight contiguous 305-m-long sections that constituted the entire length of South Branch Creek, a limestone stream in southeastern Minnesota. Total trout densities increased from about 1600/ha in 1980 to 2300/ha in 1982. There were large and significant differences in density among sections; relative differences among sections, however, were nearly constant over the 3 yr. Mean annual standing stock and production increased over the 3 yr from about 90 and 100 kg/ha, respectively, in 1980 to 150 and 174 kg/ha, respectively, in 1982. Standing stock and production also differed significantly among sections, but relative differences among sections were fairly constant over the 3 yr. The most productive sections had standing stocks and production rates that were 1.5–2 times higher than the least productive sections. Year strongly influenced growth rate, with growth in 1982 almost double that in 1981, but growth rates did not differ significantly among sections. Habitat differences among sections appeared to regulate density, size, standing stock, and production. Factors that affected the entire stream influenced recruitment and growth.

La dynamique de la production d'une population de truite brune (*Salmo trutta*) à l'état sauvage a été examinée pendant 3 an dans chacune des 8 sections contiguës longues de 305 m chacune et qui constituaient ensemble le ruisseau South Branch, un cours d'eau sur fond calcaire du sud-est du Minnesota. La densité totale de truites est passée d'environ 1600 ha en 1980 à 2300 ha en 1982. Il existait d'importantes différences de densité, significatives, entre les sections; cependant, les différences relatives entre sections sont restées presque constantes pendant les 3 an d'étude. La biomasse annuelle moyenne et la production se sont accrues pendant les 3 an, de 90 et 100 kg/ha (respectivement) en 1980 à 150 et 174 kg/ha (respectivement) en 1982. La biomasse et la production ont également différé de façon significative entre les sections, mais les différences relatives entre sections sont restées assez constantes durant les 3 an. Les sections les plus productives avaient des biomasses et des taux de production qui étaient 1,5 – 2 fois supérieurs à ceux des sections les moins productives. L'année a exercé une forte influence sur le taux de croissance, celui de 1982 étant presque le double de celui de 1981; cependant, les taux de croissance n'ont pas différé significativement d'une section à l'autre. Les différences d'habitat entre sections paraissaient réguler la densité, la taille, la biomasse et la production. Les facteurs qui agissaient sur l'ensemble du cours d'eau influençaient le recrutement et la croissance.

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Most studies of salmonid production dynamics have considered relatively short reaches of stream (300 m or less) and only a few studies have attempted to sample a substantial portion of a whole stream (Allen 1951; Chapman 1965; Hunt 1974) or have considered differences among sections of the same stream (e.g. Egglishaw and Shackley 1977). Hunt (1974) concluded that estimates of brook trout (*Salvelinus fontinalis*) production in one section of stream should not be extrapolated to the whole stream. Furthermore, consideration of production dynamics in different sections within a whole stream over time permits an examination of the relative importance of temporal (yearly) and spatial (sectional) variability in population parameters.

The factors influencing production dynamics and the responses of a population to these factors may be different between temporal and spatial scales (Rahel et al. 1984; Yant et al. 1984; Carpenter and Kitchell 1987). Yearly variation in such factors as discharge or temperature will likely influence the whole stream population and result in yearly variation in recruitment and growth (Waters 1983; Rahel et al. 1984; Yant et al. 1984). Spatial variation in factors such as habitat quality may have a greater influence on density and standing stock. These local differences in environmental factors might remain relatively constant over time, however, and the importance of spatial variation within a stream may still be dependent on whole stream or temporal responses.

The present study considers production and population dynamics of wild brown trout (*Salmo trutta*) for 3 yr, in an entire stream, divided for study purposes into eight contiguous 305-m sections. Our primary objective was to determine the relative importance of differences in population parameters

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among stream sections over time and to determine which parameters were more influenced by temporal or spatial factors. Specifically, we will test for spatial and temporal constancy in recruitment, density, standing stock, growth, and production and show that recruitment and growth are more influenced by whole stream temporal variability, whereas density, standing stock, and production are also determined by spatial (habitat) variability.

## Materials and Methods

### Study Area

South Branch Creek (43°37′N, 90°13′W; section 25, Range 12W, Township 102N, Fillmore County, Minnesota) is located in the karst topography of the driftless area of southeastern Minnesota. The stream, also known as Canfield Creek, originates from a limestone cave and flows 2.5 km north to the South Branch of the Root River. Total gradient was less than 1% and mean width was 9.6 m. The upstream half of the stream is within the Richard J. Dorer Memorial Hardwood State Forest and the lower half within Forestville State Park. Normal summer discharge ranged from 0.01–0.02 $m^3/s$ at the source to 0.2–0.3 $m^3/s$ near the mouth. Numerous springs near the cave source increased flow to about 0.1 $m^3/s$ within the first 300 m. Water from the cave source and nearby springs had a constant temperature of 9°C. The highest recorded stream temperature was 16°C at the mouth when the air temperature was 32°C. More typically, maximum temperatures at the stream mouth were below 13°C in the summer. Alkalinity ranged from 245 to 265 mg/L ($CaCO_3$), pH from 8 to 9, conductivity from 620 to 720 mS/cm, and nitrate nitrogen from 4.5 to 7.5 mg/L. No downstream trends were found for alkalinity, pH, conductivity, or nitrate concentration.

The entire valley is hardwood forest (primarily elm, *Ulmus* sp.) and the banks are shaded. However, because of the width (9.6 m) and relative shallowness of the stream, dense growths of macrophytes (primarily *Ranunculus* sp.) develop in the riffles, glides, and shallow areas of pools. Macrophyte densities varied from year to year, apparently in response to the intensity of early spring and summer floods. Macrophyte coverage in riffle and glide areas (visual estimates of percent bottom coverage) was highest in June 1981, with over 70% coverage. Coverage in 1981 was reduced by a mid-July flood to levels typical of 1980 and 1982 (25–35%). The high densities of *Ranunculus* may be related to the relative width of the stream and high spring insolation and the high nitrate levels. Watercress (*Nasturtium officinale*) occurred in some areas, primarily upstream sites, but was not nearly as abundant as *Ranunculus*.

The stream bed was composed of limestone with some sandstone. The substrate was primarily flat limestone pebbles and cobbles, interspersed with some gravel and boulders. Pools and macrophyte beds collected silt, more so in early 1981, when lack of early flooding permitted accumulation.

Slimy sculpins (*Cottus cognatus*) were abundant throughout the stream. Population estimates on selected areas in early spring and summer indicated a mean density of 8000/ha with a biomass of 63.7 kg/ha (wet weight). White suckers (*Catostomus commersoni*) were abundant but were patchy in distribution and usually occurred in pools. Other species present but not abundant were (in order of decreasing abundance) *Rhinichthys cataractae*, *Culea inconstans*, *Lepomis cyanellus*, and *Lampetra appendix*. The macroinvertebrate community was composed primarily of dipterans (chironomids, simuliids, and tipulids), mayflies (*Baetis* and *Ephemerella*), caddisflies (hydropsychids, *Brachycentrus*, and *Glossosoma*), gastropods, and oligochaetes.

TABLE 1. Mean width and percentage riffle, glide, and pool (as defined by Platts et al. 1983) for each section. Section 1 is upstream; section 8 is downstream. Percentages are based on length within each section.

| Section | Riffle (%) | Glide (%) | Pool (%) | Mean width (m) |
|---|---|---|---|---|
| 1 | 22 | 56 | 22 | 10.1 |
| 2 | 37 | 43 | 20 | 8.7 |
| 3 | 36 | 30 | 34 | 10.0 |
| 4 | 21 | 62 | 16 | 9.4 |
| 5 | 15 | 55 | 30 | 9.4 |
| 6 | 58 | 36 | 6 | 9.1 |
| 7 | 31 | 34 | 35 | 9.2 |
| 8 | 60 | 34 | 16 | 10.9 |

Since 1975 the stream has been managed as a wild brown trout fishery, with only one stocking of 2000 fingerlings in 1977 after several years of reproductive failure. The brown trout population had been increasing from low levels during the mid-1970s, when annual stocking of catchable trout ceased.

### Sections

The stream was marked out into eight contiguous sections, each 305 m long. There were differences in habitat and physiography among the eight contiguous sections (Table 1). We categorized riffles, pools, and glides (runs) according to the criteria of Platts et al. (1983). Only temperature and discharge showed any consistent trend (increasing) with distance downstream.

Section 1 began at the cave mouth as a series of riffles and pools.The lower 150 m of the section was a deep (>0.7 m) glide with low current velocity. The substratum in this reach of the section was limestone bedrock, overlain with varying accumulations of silt, sometimes in excess of 0.5 m deep. This lower portion of section 1 was the poorest reach of trout habitat in the stream and did not have a high density of fish. Riffles and pools in the upper part of the section provided good habitat and contained most of the trout in the section.

Section 2 was characterized by two large pools with alternating riffles and fast-deep glides. Section 3 comprised three large pools with an even distribution of riffles and glides. Section 4 had only three small pools. The lower 165 m of section 4 was a shallow (<0.5 m) glide, 10 m wide. This reach typically had high densities of *Ranunculus* (up to 70% coverage) which often accumulated silt. Section 5 was primarily composed of fast, deep glides with short riffle-pool segments. Section 6 lacked large pool areas and had mostly riffle-glide reaches. A large 35-m-long pool was present in section 7, just downstream from section 6. This pool and two other large pools resulted in section 7 having the highest percentage pools (35%). The section had similar percentage riffles and glides, however, and had the most even distribution of habitats of all sections (Table 1). Section 8 lacked large deep pools and was composed mainly of shallow glides and wide riffles.

### Population Sampling

Population estimates were made with the single-census Petersen mark–recapture method (Ricker 1975). Trout were sampled

with 250-V D.C. electrofishing gear on seven occasions from April 1980 to June 1983. One spring estimate (last 2 wk of April except for 1983, when high water prevented sampling until early June) and one late summer estimate (last week of July or first week of August) were made each year. On each occasion, electrofishing started at the downstream end of section 8 and proceeded upstream. Fish captured on the first, or marking, run were measured to the nearest 1 mm and were marked (temporary dorsal or ventral caudal fin clip) during the first 2 d of sampling; sections 8–5 were sampled on the first day and sections 4–1 on the second day. We resampled for the recapture run the following 2 d, again starting at section 8. Thus, four sections were electrofished each day. All data were recorded separately for each section.

On either the mark or recapture run, a stratified subsample of fish was also weighed (wet), and scales were taken from fish larger than 10 cm for age determination. Generally, two fish from each 0.2-cm size group were sampled for age and weights; typically this procedure resulted in over 200 fish sampled for age and weight on each estimate. Fish less than 10 cm were weighed and assigned to either age I (for spring sampled fish) or age 0 (late summer fish), because it was apparent from length frequency distributions that these were the correct ages. We did not handle young-of-the-year fish in the spring because they were too small (<3 cm) to be sampled effectively. Weight and age samples were taken throughout the stream, and sections were recorded for all fish weighed and aged. Additional details on age determination were given by Newman and Weisberg (1987).

## Estimation

Most estimation methods used were described by Newman and Martin (1983). Additional detail and the computer programs which were used to compute the estimates are presented, with documentation, in Newman (1985). All estimates involving weight are for wet weight. Annual estimates for the spring to spring period are attributed to the year of the first spring (i.e. 1980 production is for April 1980 to April 1981).

Population estimates were made for each sampling occasion with a modified single-census mark–recapture method, stratified by 2-cm size groups to reduce sampling bias (Newman and Martin 1983). The population size $N$ of each section was estimated from the modified Petersen formula: $N = (M + 1)(C + 1)/(R + 1)$, with variance estimated by $V(N) = [N^2(C - R)]/[(C + 1)(R + 2)]$ (Ricker 1975), where $M$ is the number of fish marked, $C$ is the number of fish captured in the second sample, and $R$ is the number of fish recaptured. These equations were used rather than those presented by Newman and Martin because of lower sample sizes encountered for some size groups within some sections. Age-specific estimates were made by using the estimated proportion of fish of a given length for that age (Newman and Martin 1983).

Apparent growth rates (Ricker 1975) for year-classes were estimated in both length and weight, based on comparison of mean size at successive sampling dates. Mean length of an age group on each date was estimated by weighting the midlength of each 2-cm size group by the population estimate for that age and size, summing over sizes, and dividing by the total number of fish of that age. The use of the midlength ignores the precision of the actual measurements and assumes that abundance is evenly distributed over the 2-cm range. This method permits the estimated abundance of each length to be used as a weighting factor. Other researchers (e.g. Avery 1983) have used this method, and the lengths were relatively evenly distributed within a 2-cm range. Mean weights for size and age groups were estimated following Garman and Waters (1983) and Newman and Martin (1983). Instantaneous growth rates were estimated as $[\ln(wt_{t+1}) - \ln(wt_t)]$ using the jackknife methods of Newman and Martin (1983).

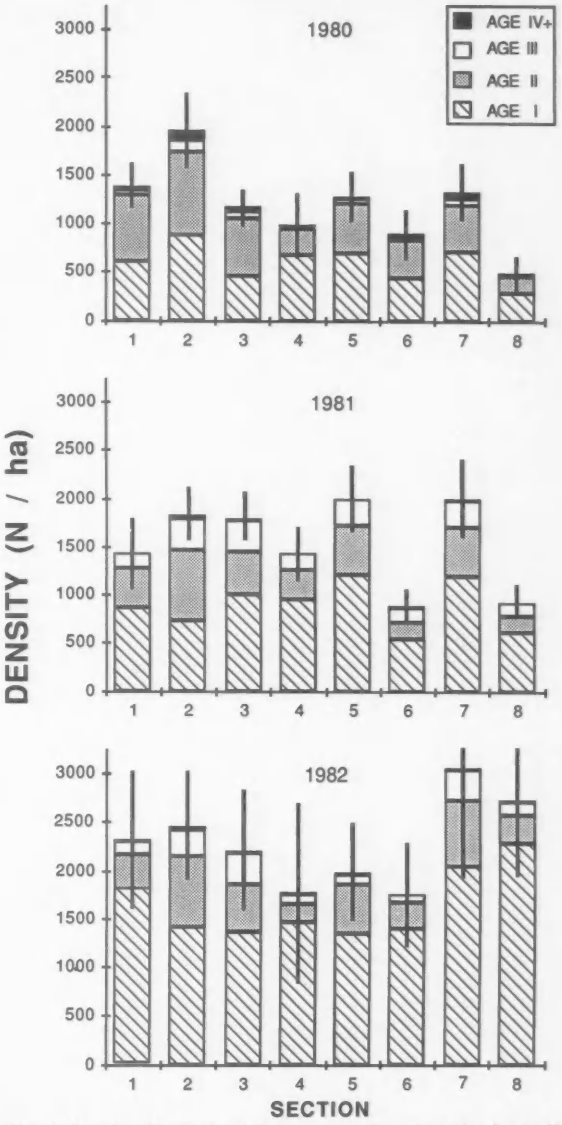


FIG. 1. Density of brown trout, by age group, in each section for April 1980 (top panel), April 1981 (middle panel), and April 1982 (bottom panel). Vertical bars represent ±2 SE for the total population.

Standing stock and production were estimated by the age-based instantaneous growth method. Estimates computed by the increment summation and size frequency methods (Garman and Waters 1983, Newman and Martin 1983) compared well with the instantaneous growth method estimates (usually within 15%). Production of young-of-the-year during the interval from

hatching to late summer was estimated as the standing stock at the late summer sampling date (see Waters 1983). This method likely underestimates production but avoids the major uncertainties of back-calculating hatching density and mortality. Production estimates based on back-calculated growth and mortality rates for young-of-the-year were less than 10% higher than estimates based on August standing stock (Newman 1985). This result suggests that we are not seriously underestimating annual production.

The methods of Newman and Martin (1983) were used for computing sampling variances and standard errors of density, standing stock, growth, and production. Because the sections were the same length, and because mean width did not vary greatly among sections (usually <15%), the estimates are reported for an equal area of 0.29 ha. This permits sectional comparisons based primarily on equal length, which may be a more meaningful scale (Hunt 1971). The use of equal areas generally resulted in less deviation among sections than would occur based on differing areas.

Because each section was sampled on each date, the data can be cross-classified by section, season, and year. Therefore, ANOVAs with eight sections, two seasons, and 3 yr as main effects were used to investigate differences among sections. Transformations were performed when needed to meet assumptions of normality (residual plots) and homogeneity of variance (Bartlett's test). The June 1983 results were not included (except for interval and annual estimates such as production) because this sample was substantially later than the other spring samples and its exclusion permitted a balanced analysis. Ranking of the sectional means was not affected by this exclusion (Spearman correlation, all $p < 0.001$). These analyses ignore the sampling variability inherent in each estimate, but they include variability due to temporal and spatial effects and the two-way interaction of these effects. In conjunction with the sampling variances, the ANOVAs presented a reasonable interpretation of the significance of the main effects and interactions. The interactions are of special interest because they indicate constancy or lack of constancy between main effects.

## Results

### Density

Densities of fish generally increased over the 3 yr (Fig. 1) but were strongly influenced by recruitment (and therefore also season); the 1981 year-class was especially strong. There were large differences in density among sections (Table 2), but relative differences remained constant over time (Fig. 1). Sections 2, 5, 7 generally had the highest densities of fish, whereas sections 6 and 8 had the lowest densities (Table 2).

The total density of fish (all age groups) varied significantly among years, seasons, and sections (ANOVA; Table 3). Relative differences among sections were fairly constant among years and seasons, as indicated by the lack of significant section × year and section × season interactions and the low percent of total variation that these interactions accounted for (Table 3). The large 1981 year-class resulted in a significant season × year interaction; young-of-the-year recruitment differed greatly among years.

Because young-of-the-year density in August had a large effect on total density, an analysis was done with all age groups except young-of-the-year. Substantial differences among sections, seasons, and years remained (Table 3). Among sections, the ratio of highest to lowest density ranged from 1.6 in August 1982 to 4 in April 1980. Over the 3 yr, section 7 had the highest mean density (1968/ha; excluding young-of-the-year) whereas section 6 had the lowest density (1176/ha; excluding young-of-the-year). Although absolute differences

TABLE 2. Mean annual density (*N*/ha), mean annual standing stock (*B*, kg/ha; wet), and annual production (*P*, kg/ha; wet) of brown trout in South Branch Creek. Production for 1982–83 is based on "uncorrected" production (410 d); "corrected" annual values can be obtained by multiplying by 365/410.

| | 1980–81 | | | 1981–82 | | | 1982–83 | | | Mean | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Section | *N* | *B* | *P* | *N* | *B* | *P* | *N* | *B* | *P* | *N* | *B* | *P* |
| 1 | 1311.7 | 87.2 | 99.4 | 3486.3 | 80.2 | 91.3 | 1909.0 | 112.1 | 162.2 | 2235.7 | 93.2 | 117.6 |
| 2 SE | 223.0 | 8.4 | 14.2 | 760.1 | 10.1 | 17.3 | 227.2 | 13.4 | 38.7 | | | |
| 2 | 1885.3 | 139.4 | 145.8 | 3272.5 | 144.4 | 130.2 | 2152.6 | 176.1 | 223.5 | 2436.8 | 153.3 | 166.5 |
| 2 SE | 258.6 | 13.1 | 19.0 | 601.6 | 15.9 | 21.5 | 177.2 | 16.1 | 88.0 | | | |
| 3 | 1692.1 | 102.2 | 104.9 | 3497.9 | 131.7 | 118.7 | 1820.8 | 142.0 | 178.5 | 2336.9 | 125.3 | 134.0 |
| 2 SE | 500.3 | 9.9 | 14.5 | 546.1 | 19.7 | 20.0 | 168.6 | 16.1 | 41.0 | | | |
| 4 | 2150.2 | 66.6 | 99.1 | 2690.2 | 81.6 | 95.7 | 2057.3 | 108.7 | 158.0 | 2299.2 | 85.6 | 117.6 |
| 2 SE | 597.3 | 9.1 | 15.1 | 547.2 | 11.9 | 18.6 | 246.4 | 17.3 | 26.1 | | | |
| 5 | 2009.2 | 96.6 | 118.7 | 5261.5 | 125.8 | 151.1 | 2504.3 | 167.9 | 223.5 | 3258.3 | 130.1 | 164.4 |
| 2 SE | 272.1 | 13.1 | 18.4 | 1713.2 | 20.1 | 29.0 | 213.5 | 15.6 | 59.0 | | | |
| 6 | 1213.7 | 61.0 | 71.6 | 2329.1 | 67.6 | 85.8 | 2058.8 | 138.5 | 179.9 | 1867.2 | 89.0 | 112.4 |
| 2 SE | 172.9 | 8.6 | 11.6 | 476.9 | 10.5 | 14.2 | 240.1 | 21.6 | 29.3 | | | |
| 7 | 1697.0 | 123.9 | 123.3 | 3497.2 | 167.1 | 152.9 | 2719.1 | 204.7 | 258.5 | 2637.8 | 165.2 | 178.2 |
| 2 SE | 206.8 | 13.7 | 17.5 | 631.1 | 16.3 | 31.2 | 256.4 | 18.2 | 40.8 | | | |
| 8 | 1186.2 | 63.5 | 72.6 | 3094.7 | 81.7 | 97.2 | 2206.6 | 113.4 | 174.1 | 2162.5 | 86.2 | 114.7 |
| 2 SE | 63.6 | 6.3 | 10.0 | 647.8 | 7.6 | 15.4 | 343.9 | 9.9 | 26.5 | | | |
| Mean | 1643.2 | 92.6 | 104.4 | 3391.2 | 110.0 | 115.4 | 2178.6 | 145.4 | 194.8 | 2404.3 | 116.0 | 138.2 |

TABLE 3. Percentage of variation (sums of squares) attributed to the 8 sections, 3 yr, and two seasons and the two-way interactions among these (ANOVA). $N1$ = abundance of all fish; $N2$ = abundance of all fish except young-of-the-year; $w$ = mean weight of all fish; $B$ = standing stock; $G_0$ = growth rate of age 0 fish; $G_I$ = growth rate of age I fish; $G_{II}$ growth rate of age II fish; $P$ = annual production; $P/B$ = annual $P/B$ ratio. Significance levels are indicated with asterisks (* $p < 0.05$; ** $p < 0.005$). N/A = not applicable.

| Term | $N1$[a] | $N2$[a] | $w$ | $B$ | $G_0$ | $G_I$ | $G_{II}$ | $P$ | $P/B$ |
|---|---|---|---|---|---|---|---|---|---|
| Section | 6.3* | 23.3** | 21.1** | 39.7** | 1.6 | 0.4 | 0.8 | 17.9** | 43.2** |
| Season | 38.7** | 6.5** | 13.7** | 14.2** | N/A | 11.9** | 52.3** | 0.2 | N/A |
| Year | 22.4** | 52.8** | 4.0* | 15.7** | 95.0** | 45.9** | 32.8** | 44.6** | 40.9** |
| Section × season | 4.7 | 0.6 | 2.0 | 3.2 | N/A | 4.8 | 1.9 | 1.0 | N/A |
| Section × year | 6.8 | 9.7* | 7.3 | 7.8 | N/A | 2.0 | 1.5 | 3.5 | N/A |
| Season × year | 17.6** | 3.5* | 48.2** | 8.6** | N/A | 30.3** | 1.6 | 31.0** | N/A |
| Error | 3.5 | 3.8 | 3.9 | 4.1 | 3.4 | 4.6 | 9.1 | 1.8 | 15.9 |

[a]$\text{Log}_e$ transformed.

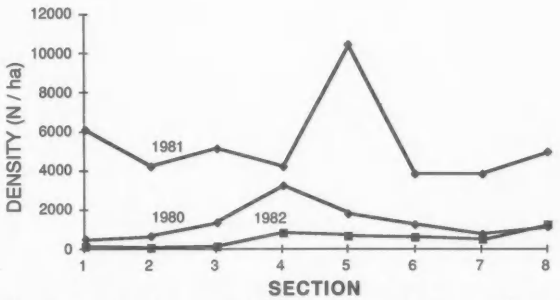


FIG. 2. Density of young-of-the-year brown trout in each section for August in 1980, 1981, and 1982.

between sections were highest at high densities, percentage deviations were higher at lower densities. Because the effects of variable recruitment were reduced when young-of-the-year fish were not included, the differences among sections accounted for more of the total variation (23% of total sums of squares; Table 3).

We investigated differences among sections, seasons, and years by age group, which is also indicative of size. Density of age 0 trout varied considerably among years and sections (Fig. 2). There were no downstream trends in young-of-the-year density. Sections 4 and 5 typically had the highest recruitment, whereas sections 2 and 7 had the lowest recruitment. Section 5 had exceptional recruitment in 1981, with over 10 000 young-of-the-year/ha (Fig. 2). There was a highly significant difference in densities among years ($p < 0.005$; Table 3), but no significant differences among sections ($p > 0.05$). Year-to-year variability in recruitment masked any differences among sections.

Density of age I fish in April increased over the 3 yr (Fig. 1), from annual means of about 560/ha in 1980 to 1600/ha in 1982. Densities were always somewhat lower in August than April, reflecting summer mortality. There were large differences in densities among sections (Fig. 1). The sections with the highest densities, 5 and 7, held substantially more age I fish (about 1050/ha, 3-yr mean) than the lowest density sections 3 and 6 (725/ha). Density of age II and III fish in April (Fig. 1) also increased over the 3 yr and there were substantial differences in density among sections. Sections 4 and 8 typically had 170–350 age II fish/ha and 40–150 age III fish/ha, whereas sections 2 and 7 usually had 500–700 age II fish/ha and typically more than 200 age III fish/ha.

There were significant differences among years and among sections for densities of age I, age II, and also age III fish (ANOVA; all $p < 0.05$). Densities of age I and III fish also were significantly different among seasons (ANOVA; both $p < 0.01$). Differences among sections explained from 11% (age I) to 63% (age II) of the total variation (% sum of squares), and differences among years explained from 5% (age II) to over 40% (ages I and III) of the total variation. Season effects never accounted for more than 12% of the total variation. Furthermore, relative differences among sections remained fairly constant over time; none of the section × season interactions were significant ($p > 0.05$) and the section × year interaction was significant only for age I fish ($p < 0.05$). Season × year interactions were significant for all three age–groups ($p < 0.01$), reflecting variable recruitment. None of the two-way interactions explained more than 12% of the total variation.

## Standing Stock

There were large differences in standing stock among sections (Fig. 3). The ratio of highest to lowest standing stock (among sections) was usually ≥2 (Table 2) and differences among sections accounted for 40% of the total variation (Table 3). Furthermore, relative differences among sections did not change over years or seasons, as indicated by the lack of significant section × year and section × season interactions (Table 3). For example, over the 3 yr, sections 4 and 8 had mean standing stocks of about 85 kg/ha whereas sections 2 and 7 typically had standing stocks ≥140 kg/ha.

## Size

Mean weight (grams wet weight) was estimated as the standing stock divided by the density of fish (number per hectare). This estimate is indicative of overall size of fish, not growth. Mean weight in each section was higher in April (range among sections from 28 to 86 g) than August (14–81 g) during 1980 and 1981. Low recruitment in 1982 resulted in higher values in August 1982 (36–81 g) than April 1982 (28–52 g). There were large differences among sections (see Table 2). For example, over the 3 yr, section 4 had mean weights from 15 to 56 g whereas sections 2 and 7 typically had mean weights from 30 to 80 g.

Significant differences in mean weight among sections, seasons, and years explained 21, 14, and 4% of total variation, respectively (Table 3). The highly significant season × year interaction that explained 48% of the total variation was primarily due to the influence of the abundant 1981 year-class. The lack of significant section × year and section × season interactions (Table 3) indicated that mean size may also be a relatively constant property of each section.

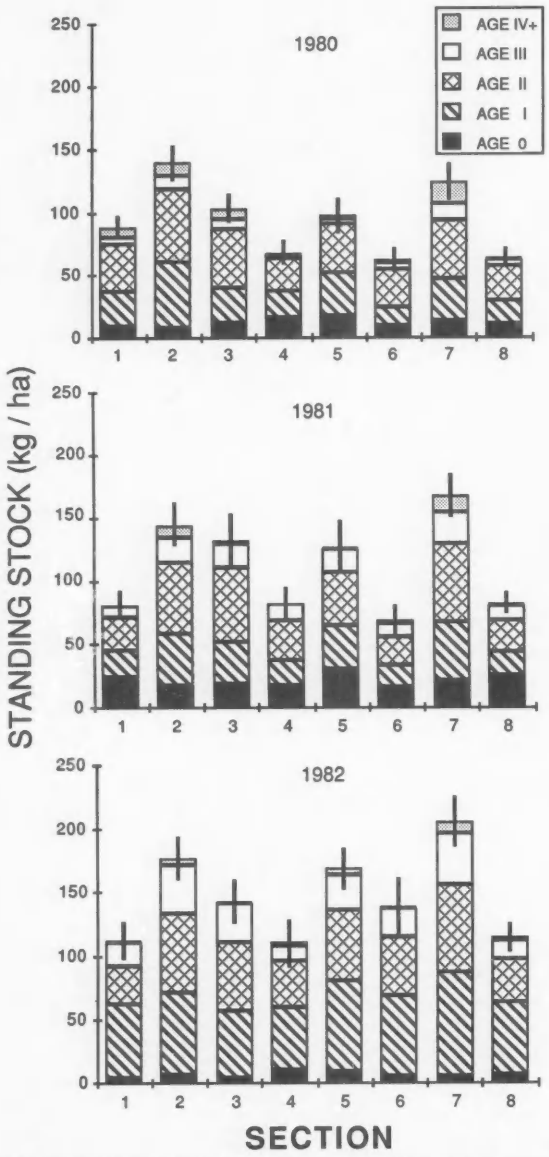


FIG. 3. Mean annual standing stock (wet) of brown trout, by age group, in each section for 1980–82. Vertical bars represent ±2 SE for the total population.

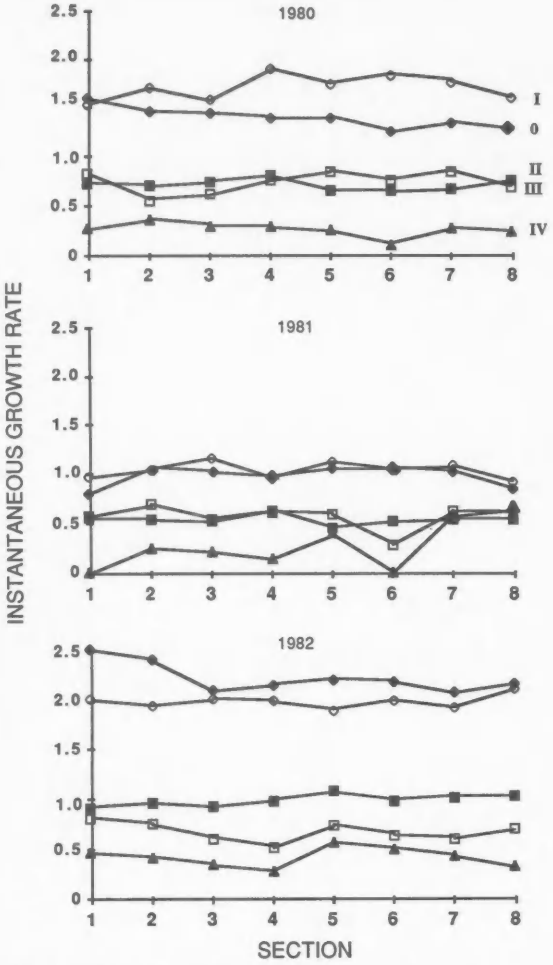


FIG. 4. Annual instantaneous growth rates of brown trout, by age group, in each section for 1980–82.

## Growth

Annual instantaneous growth rates were much lower in 1981 than in either 1980 or 1982 (Fig. 4). Although there were large seasonal and yearly differences in growth within sections, no significant differences were found among sections (Table 3). Similar results were found for absolute growth in length; section effects and section interactions were not significant.

It should be noted, however, that among sections, the growth rate of a given age group for a specific interval (e.g. April–August 1981) sometimes varied substantially; there were up to twofold differences which were significantly different based on sampling error (sensu Newman and Martin 1983). For example, the April–August 1981 growth rate of age I fish in section 7 ($G = 0.977 \pm 2$ SE $= 0.141$) was significantly higher than in section 1 ($G = 0.59 \pm 0.228$), based on sampling error. In general, however, differences between samples were not significant. The lack of significant differences among sections indicated by ANOVA was due to a lack of consistent differences among sections rather than a lack of variability.

## Production

Annual production in the entire stream and in most sections increased over the 3 yr; whole stream production increased from 104 kg/ha in 1980 to 115 kg/ha in 1981 and 195 kg/ha in 1982 (175 kg/ha corrected to 365 d). Differences among sections were quite large (Fig. 5); the ratio of highest production to lowest production was about 2 in all 3 yr. In general, sections 2, 5, and 7 always had the higher production, and section 3 intermediate production, whereas sections 1, 4, 6, and 8 typically had low rates of production (Fig. 5).

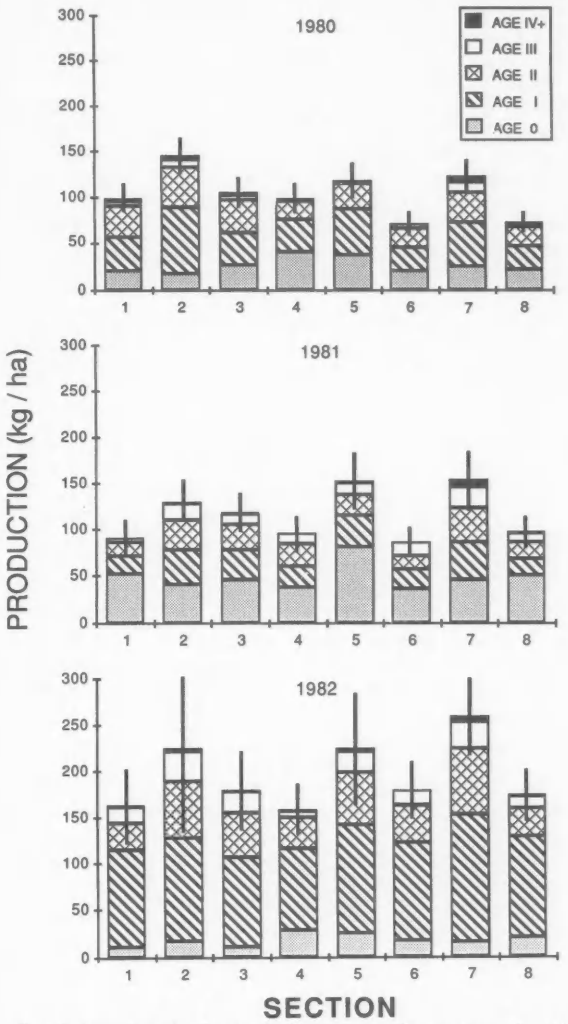


FIG. 5. Annual production (wet) of brown trout, by age group, in each section for 1980–82. Vertical bars represent ±2 SE for the total population.

TABLE 4. Annual *P/B* ratios of brown trout in each section for 1980–83. Values for 1982–83 are based on "uncorrected" production (410 d); "corrected" values can be obtained by multiplying by 365/410.

| Section | 1980–81 | 1981–82 | 1982–83 |
|---|---|---|---|
| 1 | 1.14 | 1.14 | 1.45 |
| 2 | 1.05 | 0.90 | 1.27 |
| 3 | 1.03 | 0.90 | 1.26 |
| 4 | 1.49 | 1.17 | 1.45 |
| 5 | 1.23 | 1.20 | 1.33 |
| 6 | 1.17 | 1.27 | 1.30 |
| 7 | 1.00 | 0.92 | 1.26 |
| 8 | 1.14 | 1.19 | 1.54 |

Among the eight sections and 3 yr, there were significant differences in annual production among both sections and years, with differences among sections explaining over 27% of the total variation. Analysis with seasonal production (April–August and August–April) over the 3 yr and eight sections showed significant section and year differences, but no differences between seasons (Table 3). These results indicated significant differences among sections, but the lack of significant interactions of section with year or season (Table 3) indicated that relative differences among sections were fairly constant over time (Fig. 5).

### Annual Production to Biomass (P/B) Ratios

Annual P/B ratios were higher in 1982 than in 1980 and 1981 (Table 4). There were, however, also consistent differences among sections, with sections 1, 4, and 8 having high P/B ratios and sections 2, 3, and 7 having low ratios. P/B ratios were not constant among sections or years (Table 3); year and section effects each explained over 40% of the total variation.

### Relationship of Growth and Density

The reduced growth rates observed during the 1981–82 period, concomitant with the strong 1981 year-class, suggested that there may be a density-related effect on growth among sections. For each sampling interval, Spearman and Pearson correlations were computed, by age group, for mean density during the interval and growth rate during the interval among sections (eight pairs for each correlation); correlations with age 0 fish were only computed for the August–April interval. Of the 21 correlations, only the Spearman correlation for the 1981 year-class during August 1982 to June 1983 was significant ($p < 0.05$; Spearman $r_S = -0.762$). About half of the correlations were positive, indicating that among sections, growth of a year-class was usually not negatively correlated with its density. When the data for each season were combined over years (24 pairs for each correlation), the only significant correlations were a positive correlation for age I fish ($r_S = 0.617$) and a negative correlation for young-of-the-year ($r_S = -0.920$). The density-dependent correlation for young-of-the-year was primarily due to the large yearly differences in growth and density rather than density dependence among sections within years.

Correlations of total standing stock (both initial and final) and growth rates of age 0, I, and II fish were also computed for each sampling interval. Negative correlations would indicate that growth was negatively related to total population biomass within a section. None of the correlations were significant (all $p > 0.05$) for either the winter or summer growth intervals. Furthermore, about half of the correlations were positive, again suggesting that there is no density-related differences in growth among sections.

## Discussion

Differences among sections were noted for all population parameters except growth. These differences were detectable even though most of these parameters were changing over the 3 yr and major changes in recruitment occurred. In general, the relative differences among sections remained constant over time, indicating that the differences were a result of sectional properties and not stochastic or sampling variations.

Total fish density in South Branch Creek was strongly influenced by young-of-the-year recruitment, which appeared to be

determined by abiotic rather than biotic factors (Newman 1985). However, total densities within sections were not directly determined by recruitment within the sections. Dispersal to and from sections by young fish probably occurred. Year-to-year variation was more influential than sectional differences for age 0 and I fish and was substantial for age III fish, and also age II fish when June 1983 was considered. Somewhat surprisingly, late summer versus spring effects were generally influential only because they reflected recruitment; the relatively low mortality in the population resulted in year-to-year stability of the older age groups. Even with the large year-to-year changes in whole stream density, consistent differences among sections were found.

Some differential dispersal of younger age or size groups also occurred among sections. Some sections, for example section 4, appeared to have high emigration of young-of-the-year fish by the following spring, while other sections (e.g. 1 and 2) often had more yearlings than young-of-the-year of the same year-class. Hunt (1974) also reported dispersal for young brook trout, as have Milner et al. (1978), Mortensen (1982), and Crisp et al. (1984) for brown trout. However, these studies have generally reported a downstream dispersal. In South Branch Creek, and in several streams studied by Crisp et al. (1984), some young fish moved upstream to sites with low recruitment. There was, however, little evidence of consistent movement by the older fish.

There was considerable year-to-year variation in population age structure, but population structure within sections was still relatively constant (Fig. 1). These results support suggestions that carrying capacity may be determined by available habitat and possibly foraging sites, with migration to and retention within sections having available suitable habitat (e.g. Chapman 1966; Hunt 1971; Bachman 1982, 1984). Furthermore, the amount of suitable habitat available may be size or age dependent (Bohlin 1978), resulting in different size or age structure among sections.

Much of the segregation among sections was based on size; some sections (e.g. 4) typically had a lower mean weight for all trout whereas other sections (e.g. 2 and 7) had larger fish. These observations were also supported by the differences in densities of age groups among sections. Bohlin (1977, 1978) and Elser (1968) have also reported size differences among habitats. Within age groups in South Branch Creek, significant differences among sections for mean length at age were found only for age I and III fish. Differences in mean length among seasons and years were much larger, and even the significant differences among sections never explained more than 3% of the total variation. The lack of significant differences among sections in growth rate (length or weight) further indicated that differential size segregation rather than differential growth explained the mean size differences among sections. Growth was more influenced by year and season than by sectional differences. Bohlin (1977) and Elser (1968) have also concluded that segregation rather than growth results in size differences among sections of streams.

The general lack of significant correlations between density or biomass and growth among sections indicated that densities within sections did not generally regulate growth within sections. These results further support the hypothesis that densities (and biomass) are more likely to be regulated by migration or mortality (McFadden and Cooper 1964; McFadden 1969; Bachman 1982, 1984). However, the significant negative correlation for the 1981 year-class between August 1982 and June 1983 may be a true exception. If so, this would indicate that density effects among sections may not occur to detectable levels until the fish are well into their second year of growth and at high densities. There is some indication in the data of Hunt (1971) that large increases in standing stock, brought about by habitat improvement, resulted in lower growth, especially for older fish. The largest reductions occurred among years but there was some indication of a greater reduction in those sections with the largest increase in standing stock (Hunt 1971). In South Branch Creek, growth of young-of-the-year was negatively related to density over the 3 yr, suggesting that density dependence occurs among years, but not among sections. Bachman (1984) proposed that growth should vary among stream sections, but should not be density dependent. In contrast, our results show that within stream reaches of several kilometres, growth may not vary among sections, but density-dependent growth may be evident with large year-to-year variation in recruitment.

Standing stock in biomass increased over the 3 yr, was generally highest in August, and differed significantly among sections. The lack of significant section interactions indicated that relative differences among sections remained constant between seasons and years. Seasonal production also varied significantly among sections, but relative differences remained constant over time. The large increase in production and standing stock over the 3 yr was due mainly to high recruitment which resulted in increasing densities of older fish in subsequent years. During the study, the population appeared to still be expanding from the low levels found in the mid-1970s (Newman 1985).

There were no seasonal differences in production, owing to the longer interval length for August–April production; on a per-day basis, April–August production would generally be three times higher than August–April production. Throughout the study, carrying capacity and total production appeared to be related to properties of the sections, which retained their relative rankings over years and seasons. The sections, however, should not be viewed as closed or separate systems (Hunt 1974; Milner et al. 1978; Crisp et al. 1984). Some movement of young fish apparently occurred. Mass movements to and from sections did not occur, because these would result in significant section interactions over time. Rather, within the boundaries set by the whole stream population, standing stock and production adjusted accordingly across all sections and maintained their relative ranks.

Annual production generally reflected mean standing stock, but was somewhat less variable among sections. However, annual P/B ratios were not constant among sections. Because growth among sections was essentially constant, the P/B ratios were reflecting the size and age structure of the sections. The contrast among sections is interesting in light of the relative constancy in annual P/B ratios in the whole stream over the 3 yr (all about 1.1 when growth for 1983 was corrected to April, resulting in an annual production of 174 kg/ha). Other researchers (e.g. Hunt 1974; Waters 1983) have often found annual P/B ratios to vary by 20–30% over several years.

Widespread differences have been found for trout population parameters (density, growth, standing stock, and production) between different streams (e.g. McFadden and Cooper 1962; LeCren 1969; Waters 1977). Furthermore, LeCren (1969) noted that similar production rates in different streams may be reached with very different densities, growth, and standing stocks. Some streams have high densities of small but fast-growing fish whereas others have lower densities of slow-growing, but large

fish. In South Branch Creek, the relatively high production was attained by a combination of moderate to high density and standing stock and moderate growth rates.

Less information is available on temporal changes in population parameters. Hunt (1966, 1974) found a maximum difference of 20% (120–106 kg/ha) for whole stream annual production of brook trout over 11 yr; greater annual deviations were found for parameters within age groups. Egglishaw and Shackley (1977) found a difference of 60% (123–77 kg/ha) for brown trout production over 8 yr. The high and low estimates were for the consecutive years of 1967 and 1968, respectively. Waters (1983) found a maximum deviation of over 400% (44–190 kg/ha) for a mixed brook, brown, and rainbow trout (*Salmo gairdneri*) population over 15 yr. The lowest estimates were the result of several devastating floods (Elwood and Waters 1969; Hanson and Waters 1974). Comparisons among more stable years also indicated some large differences, e.g. 1978 and 1979, when production rose 70% from 113 to 190 kg/ha (Waters 1983). A minimal ratio of change in production over years for South Branch Creek was 70%, using the corrected-growth 1982 production estimate (104–174 kg/ha), again showing high year-to-year variability. In all of the above studies, variable recruitment was a primary cause of the production variation, but year-to-year differences in growth were also found.

Variation between sections within years has received even less attention. In 12 km of the Horokiwi Stream, Allen (1951) found substantial differences in density, standing stock, growth, and production of brown trout between different reaches (0.5–3 km in length). Physiography differed greatly among the reaches, and Allen considered the populations within reaches to be much more homogeneous.

Egglishaw and Shackley (1977) found large differences in brown trout density between small (<30 m in length) sections, but found small differences in growth, a result consistent with our study. Annual production varied somewhat between sections (maximum deviation 30%), but much less so than between years. In contrast with our results, section rankings in Egglishaw and Shackley's study did not appear to be constant over time, but the same sections were not reported every year, making comparisons difficult. Furthermore, the small size of the sections could result in high temporal variability due to short movements of fish or sampling error (Rahel et al. 1984; Yant et al. 1984).

Hunt (1966, 1974) examined four contiguous sections that composed the 5.4-km Lawrence Creek. As in the present study, little difference in growth among sections was found (Hunt 1966). Differences in production between sections were as high as 400% and production decreased with distance downstream. These differences were much less when based on section length rather than area, in part due to the doubling of mean width from the first to last section (Hunt 1974). However, Hunt (1971) was able to relate standing stocks in 91-m subsections to stream physiography (pools and cover). Year-to-year variation in production was higher for individual sections than for the whole stream (Hunt 1974).

In South Branch Creek, ratios of maximum to minimum section production ranged from 2:1 in 1980 to 1.6:1 in 1982. The ratios declined as total production increased, possibly indicating an approach to carrying capacity. Both Hunt's study and our study indicate that considerable differences in population parameters can occur among even large (>300 m) contiguous sections. However, although relative differences among sections appear to be fairly constant between years, the populations within sections are not entirely independent, especially for younger fish (see also table 2 of Hunt 1974). In fact, Hunt (1974) noted that the habitat improvement and the subsequent production increase in one section resulted in lower production in the other sections and little change for the whole stream. One must extrapolate estimates from a given section to the whole stream with extreme caution.

The lack of any specific downstream trends for population parameters in South Branch Creek was probably due to the lack of regular changes in the physiography, species composition, and also the shortness of the stream. Mean width, for example, changed little with distance downstream whereas in Lawrence Creek, mean width more than doubled (Hunt 1974). Waters (1981) found that invertebrate drift in South Branch Creek increased rapidly downstream from the cave source and appeared to level off in the first several 100 m, rather than increasing linearly downstream. Other studies (e.g. Elser 1968; Lewis 1969) have found that habitat differences were of primary importance and have noted no additional downstream effects.

Numerous physical factors such as percent cover, percent pools, and mean depth have been shown to influence fish density and standing stock in streams (Elser 1968; Lewis 1969; Hunt 1971; Bohlin 1978; Hartzler 1983; Bowlby and Roff 1986). We computed correlations for the physical parameters of each section (percent riffle, pool and glide, and mean width; Table 1) with various trout population parameters for each section and sampling date (total density, density of age groups, standing stock, mean weight, and production). Percent pools was the only factor that had significant correlations (all positive). Only total density and mean standing stock were significantly correlated with percent pools at the 0.05 level, and production was significant at the 0.01 level.

Several authors have found that pool area is an important determinant of trout density or standing stock (e.g. Hunt 1971; Bohlin 1978; Bowlby and Roff 1986). Bohlin (1978) determined that pools were important for age II and older trout; however, riffle areas were also important for young fish. In the present study, young-of-the-year and yearling fish within sections were typically associated with riffle areas and shallow glides containing macrophytes. Young-of-the-year parameters were not significantly correlated with any physical parameters among sections, and apparently factors not measured were more important. The lack of significant section effects for the age 0 ANOVAs further indicated that properties of the sections could not explain young-of-the-year density. Although pools were very important, increasing pool area in the high-density sections may not benefit the population. Bowlby and Roff (1986) reported a positive relationship of trout biomass with percent pools, but they also found that the lowest biomass reaches had the very highest percent pools (mean of 54%); there appears to be an optimum level of percent pools below 45%.

Several estimation problems could have an effect on our absolute results, but should not affect our interpretations. By assuming that young-of-the-year standing stock in August equals young-of-the-year production to August, we are probably underestimating annual production. However, one of us (Newman 1985) has shown, with back-calculated young-of-the-year growth and mortality estimates, that our estimates are likely not more than 10% low. Also, ANOVAs with young-of-the-year excluded gave similar results (% sums of squares) and identical interpretations (levels of significance) to the results in Table 3 for standing stock and production. Our interpretations are thus not affected by our methods of estimating young-of-the-year

production. Mass movements between sections can also influence results, especially for small sections (Milner et al. 1978). In our study, most movement appeared to be by young-of-the-year fish, as has also been shown by others for resident brown trout (e.g. Solomon and Templeton 1976; Elliott 1987). The lack of section × year and section × season interactions in our study and observations by others (e.g. Solomon and Templeton 1976; Bachman 1984) suggest little movement of the older fish. Unless fish moved often, in regular patterns, or as a result of our sampling, movement should have little effect on our interpretations. We returned sampled fish to within 3 m of the point of capture and observations during sampling did not indicate fish moving in and out of sections. Our sections were long and thus had only slight boundary effects. Furthermore, sections losing fish are expected to have reduced production relative to sections gaining fish, so movements that did occur should have little effect on our interpretations. Most likely, young fish will move to suitable habitat (Solomon and Templeton 1976) and then remain in that area as adults (Bachman 1984).

The comparisons of population dynamics among sections of South Branch Creek permit a conceptual development of trout population dynamics that may be applicable to other stream populations. Abundance of a cohort in South Branch Creek was determined by recruitment which appeared to be controlled by environmental factors such as winter flows and flooding (Newman 1985), as others have also reported (e.g. Mortensen 1982; Elliott 1985). Abundance, but not growth, was regulated among sections, probably by density-dependent relationships with suitable habitat. Furthermore, some size segregation occurred among sections. This factor was also likely related to habitat, but not growth. Growth appeared to be regulated only within the whole stream, between years and seasons. Growth regulation appeared to be both density and environmentally influenced, but only as these factors affected the whole stream over time. These results are consistent with other conceptual models of stream trout population regulation (Allen 1969; McFadden 1969) but point out the importance of temporal and spatial scale. Microhabitat (e.g. very small sections or areas) was not considered in our study, but greater temporal variation in population parameters has been shown among smaller sections (e.g. Egglishaw and Shackley 1977; Bohlin 1978). Because streams are essentially open-ended systems, numerical population regulation such as migration can be important. Within larger areas, physical constraints may reduce the effectiveness of numerical regulation; better sites may not be available. Factors that in large part influence the whole system will impose further constraints that numerical regulation alone may not ameliorate.

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# Comparative Mortality of Three Esocids due to Stocking Stressors

Martha E. Mather and David H. Wahl

*Ohio Cooperative Fish and Wildlife Research Unit,[1] Department of Zoology, The Ohio State University, 1735 Neil Avenue, Columbus, OH 43210, USA*

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For stocked sportfish, stocking stress can cause substantial mortality. We evaluated mortality of three young-of-year esocids, northern pike (*Esox lucius*), muskellunge (*E. masquinongy*), and their $F_1$ hybrid, the tiger muskellunge, in response to simulated handling, transport, and thermal stressors in the laboratory. In 15°C acclimated esocids, a 10° rapid temperature increase caused little mortality. A 12° increase killed some fish in all taxa; however, mean mortality did not differ significantly among northern pike ($\bar{X}$ = 30%), tiger muskellunge ($\bar{X}$ = 23%), and muskellunge ($\bar{X}$ = 10%). Nearly all 15°C acclimated fish (98%) died in response to a 15° increase. Tempering (0.15°·min$^{-1}$) did not reduce this near complete mortality. Handling (30 s dipnet) and transport confinement (60 g·L$^{-1}$ for 120 min) also did not alter mortality when compared with a 12° temperature increase alone. Field experiments, completed concurrently, confirmed our laboratory finding that healthy esocids, acclimated to 15°C, stocked at lake temperatures corresponding to a temperature increase ≤10°, suffered little mortality. Because mortality did not differ among these two species and their hybrid, differential vulnerability to these stocking stressors need not be considered when deciding which esocid to stock.

Chez les espèces sportives ensemencées, le stress de l'ensemencement peut provoquer une mortalité substantielle. Nous avons évalué la mortalité chez les jeunes de l'année de trois ésocidés, soit le brochet (*Esox lucius*), le maskinongé (*E. masquinongy*), et leur hybride $F_1$ par suite de leur manipulation, du transport et de stress thermiques simulés au laboratoire. Chez les ésocidés acclimatés à l'eau à 15°C, un accroissement rapide de température de 10°C a causé peu de mortalité. Un accroissement de 12°C a tué certains sujets dans tous les taxons; cependant, la mortalité moyenne n'a pas différé de façon significative entre le brochet ($\bar{X}$ = 30 %), l'hybride ($\bar{X}$ = 23 %) et le maskinongé ($\bar{X}$ = 10 %). Presque tous les poissons acclimatés à l'eau à 15°C (98 %) sont morts lors d'un accroissement de température de 15°C. Le fait d'étaler le réchauffement (0,15°C·min$^{-1}$) n'a pas réduit cette mortalité presque totale. La manipulation (carrelet 30 s) et le confinement durant le transport (60 g·L$^{-1}$ pendant 120 min) n'ont pas modifié, non plus, la mortalité obtenue par le seul accroissement de température de 12°C. Les expériences sur le terrain, faites en même temps que les expériences de laboratoire, ont confirmé les constatations faites en laboratoire, soit que les ésocidés en santé et acclimatés à l'eau à 15°C, lorsqu'ils sont introduits dans des lacs dont la température correspond à une augmentation de température de 10°C ou moins, souffrent peu de mortalité. Étant donné que la mortalité entre ces deux espèces et leur hybride n'a pas différé, on conclut qu'il n'est pas nécessaire de tenir compte de la vulnérabilité à ces stress liés à l'ensemencement lorsqu'on décide d'ensemencer un lac avec l'une ou l'autre espèce.

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Muskellunge (*Esox masquinongy*), northern pike (*E. lucius*), and tiger muskellunge, the $F_1$ hybrid of female muskellunge and male northern pike, are important sportfishes routinely stocked throughout North America (Webster et al. 1978). The stress associated with stocking causes mortality in muskellunge (Belusz 1978) and tiger muskellunge (Stein et al. 1981; Carline et al. 1986). Isolating the individual stocking stressors responsible for this mortality will aid in developing stocking techniques which maximize survival.

Mather et al. (1986), in an experimental assessment of mortality in tiger muskellunge caused by stocking stressors, found that thermal stress at stocking, not handling or confinement during transport, was critical to poststocking survival. To understand the stress response of the two species and their hybrid, the responses of northern pike and muskellunge need to be compared, simultaneously, with those for tiger muskellunge. Mather et al. (1986) also found no relationship between mortality and one physiological index of stress, plasma glucose. They concluded that this physiological index was not a good indicator of reduced survival. Given this lack of a relationship, we chose mortality at 48 h as our only index of stocking stress. Mortality in response to stress can be a complex and variable response. Small sample sizes and the use of fish sizes and temperatures outside the range used for stocking make existing data for esocids (Scott 1964; Bonin and Spotila 1978) inappropriate for a comparative assessment of response to thermal stressors.

In this study, we compare mortality among muskellunge, northern pike, and tiger muskellunge due to three stocking stressors: handling in the hatchery, confinement during transport, and temperature increase at stocking. We evaluate the use of temperature acclimation in reducing mortality caused by

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thermal stress at stocking. We also compare our laboratory findings with results from five routine reservoir stockings. With these data, we evaluate which esocid survives best under a given stocking regime and suggest guidelines for minimizing mortality during stocking for all three esocids.

## Methods

We obtained northern pike from Ohio Division of Wildlife's St. Mary's Fish Farm, St. Mary's, Ohio, and muskellunge and tiger muskellunge from London Fish Farm, London, Ohio. Young-of-year esocids ($\bar{X}$ = 48.1 g, 95% CI = 46.0–50.2 g; $\bar{X}$ = 216 mm total length) were partitioned by taxa in a 4000-L aquarium (25% water volume exchanged daily) at a fish density of 4–10 g·L$^{-1}$ during July through December 1984 and 1985. Holding conditions maintained during acclimation were 15 ± 1°C, 4–10 mg dissolved oxygen·L$^{-1}$, 5–30 mg·L$^{-1}$ total hardness (as $CaCO_3$), 0.5–1.0 mg total ammonia·L$^{-1}$, mean pH 7.4, and a photoperiod of 14 h light : 10 h dark. Esocids were fed minnows ad libitum during acclimation. The acclimation temperature used is within the range found in many spring-fed hatcheries (M. E. Mather, pers. obs.). Our decision to use a single acclimation temperature for all treatments allowed us to concentrate on rigorously testing the taxa and stressor effects. In treatments designed to test effects of temperature shock, we monitored mortality of 15°C acclimated fish in response to rapid temperature increases of 10, 12, and 15° that might occur when fish are transferred from truck to lake. We assumed that no temperature increase occurs during transport, as is the case in Ohio during routine stocking. In each experiment, we transferred 8–10 fish of each taxon from the acclimation tank to separate 110-L test aquaria initially held at acclimation temperature (test density 6–8 g fish·L$^{-1}$). Tanks were randomly assigned and all three taxa were tested simultaneously. In these three thermal-stress-only treatments, we allowed fish to recover from the handling stress associated with aquarium transfer for 24 h. No esocid mortality occurred during this recovery period in any of the experimental treatments. We then raised the temperature from acclimation to test temperature at a rate of 1.60°·min$^{-1}$ (see Mather et al. 1986 for a complete description). Because we increased water temperature with the test fish in the tank, our method is a modification of the traditional upper lethal temperature method (Brett 1952). Dissolved oxygen exceeded 5 mg·L$^{-1}$ and total ammonia ranged from 0.0 to 1.5 mg·L$^{-1}$. Because Mather et al. (1986) found that only one of all tiger muskellunge tested ($N$ = 96) died between 2 and 7 d, mortality was recorded 48 h after the test temperature was reached. The number of experimental replicates within each treatment varied with fish availability (see Fig. 1 and 2).

In the next set of experiments, we tested the combined effects of dipnet handling and temperature increase, similar to that encountered when fish are transferred from hatchery to truck. To simulate handling, we held one to six fish out of water in the dipnet (20 × 30 × 30 cm, 5-mm mesh) for 30 s, released them into the test tank, initially held at acclimation temperature, and then increased water temperature 12°. We used a 12° increase to evaluate multiple stressors because this was the only increment tested where intermediate levels of mortality occurred. In the next treatment, we added a confinement stressor, which simulated crowding during transport, to handling and thermal stressors. After the handling stressor described above, fish were confined at 60 g·L$^{-1}$ for 120 min, a density and duration that typically occur when Ohio Division of Wildlife hauls esocids. Fish then were released into test tanks and we increased temperatures 12°. To test if rate of temperature increase affected mortality, in the final treatment, we simulated tempering by reducing the rate of temperature increase from 1.60 to 0.15°·min$^{-1}$ during a 15° temperature increase. We chose a 15° increase because this was the only increment where mean mortality exceeded 50% and we hypothesized that the effect of tempering would be greatest here.

Concurrent with laboratory experiments, we monitored poststocking mortality during five stockings in three Ohio reservoirs: North Lake, Summit County; Madison Lake, Madison County; and Kokosing Lake, Knox County. At stocking, 30 fish of each taxon were confined in predator-free cages (2.6 × 0.9 × 0.9 m). Mortality was recorded after 48 h. Handling, confinement, and temperature increase occurred but the duration and magnitude of each stressor differed between the laboratory and field. In field stockings, fish were dipnetted into the truck at the hatchery (30 s) and tempered from hatchery (20°C) to lake (Table 1) over 20 min. Confinement densities during transport were similar to laboratory experiments but duration of transport varied from 1.0 to 2.5 h.

An arcsin transformation was used on percent mortality data to stabilize the variance (Steel and Torrie 1980) before statistical tests were performed. Two-way analysis of variance (ANOVA) and Tukey multiple comparisons tested differences among taxa and treatments. To test if mortality differed from zero for any individual taxon–treatment combination, we used a one-sample $t$-test.

## Results

Experimental mortality in 1984 and 1985 did not differ (ANOVA, $P > 0.05$); thus, data from both years were combined. Similar numbers of northern pike, muskellunge, and tiger muskellunge died within each of the three temperature treatments (ANOVA, $P > 0.05$; Fig. 1). Of all esocids, only 1 of 60 tiger muskellunge died by 48 h when temperatures were rapidly increased from 15 to 25°C (Fig. 1). When temperature was increased from 15 to 27°C, mortality occurred in both species and their hybrid (Fig. 1). Mean mortalities of northern pike ($\bar{X}$ = 30%) and tiger muskellunge ($\bar{X}$ = 23%) were greater than zero ($t$-test, $P < 0.05$); mean muskellunge mortality ($\bar{X}$ = 10%) did not differ from zero ($t$-test, $P > 0.05$). In all taxa, a 15° increase caused nearly complete mortality, exceeding that caused by either a 10 or 12° increase (ANOVA, $P < 0.05$; Fig. 1).

Decreasing the rate of temperature increase from 1.60 to 0.15°·min$^{-1}$ did not reduce mortality caused by a 15° increase at 48 h (ANOVA, $P > 0.05$; data not shown). After tempering at 0.15°·min$^{-1}$, fewer northern pike ($\bar{X}$ = 30%) and muskellunge ($\bar{X}$ = 75%) but similar numbers of tiger muskellunge ($\bar{X}$ = 95%) died after 4 h than in the 1.60°·min$^{-1}$ treatment ($\bar{X}$ = 98, 94, and 98%, respectively). However, in both treatments, near 100% mortality occurred in both species and their hybrid by 24 h. The exception was 3 of 60 muskellunge that survived beyond 48 h in the 1.60°·min$^{-1}$ treatment.

The two multiple stressor treatments, handling followed by a 12° temperature increase and handling followed by confinement at high density and a 12° temperature increase, did not increase cumulative mortality in any taxa when compared with a 12° increase alone (ANOVA, $P > 0.05$; Fig. 2).

TABLE 1. Percent mortality of muskellunge (MU), northern pike (NP), and tiger muskellunge (TM) held in predator-free cages for 48 h after five reservoir stockings. Fish were tempered 20 min in the transport truck before stocking. Data are mean (±1 SD) of three replicate cages at each stocking. Ten fish of each species were in each cage.

| Reservoir | Stocking date | Water temperature (°C) | Percent mortality | | |
|---|---|---|---|---|---|
| | | | MU | NP | TM |
| North | 29 Aug. 1983 | 25.0 | 0.0 | 0.0 | 0.0 |
| North | 2 Sept. 1984 | 25.0 | 0.0 | 0.0 | 0.0 |
| North | 26 Aug. 1985 | 25.0 | 0.0 | 0.0 | 0.0 |
| Kokosing | 6 Aug. 1985 | 27.0–28.5 | 3.3 (±5.8) | 0.0 | 6.6 (±5.8) |
| Madison | 30 July 1985 | 26.0–27.6 | 0.0 | 3.3 (±5.8) | 0.0 |

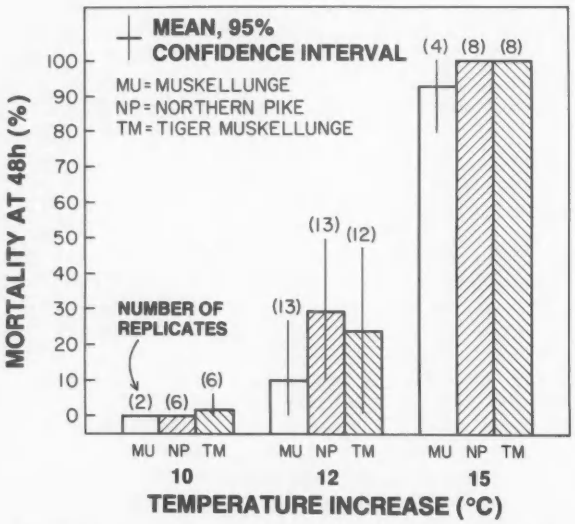


FIG. 1. Mean mortality at 48 h of 15°C acclimated young-of-year muskellunge (MU), northern pike (NP), and tiger muskellunge (TM) subjected to rapid temperature increases (1.60°·min$^{-1}$) of 10, 12, and 15° in the laboratory.

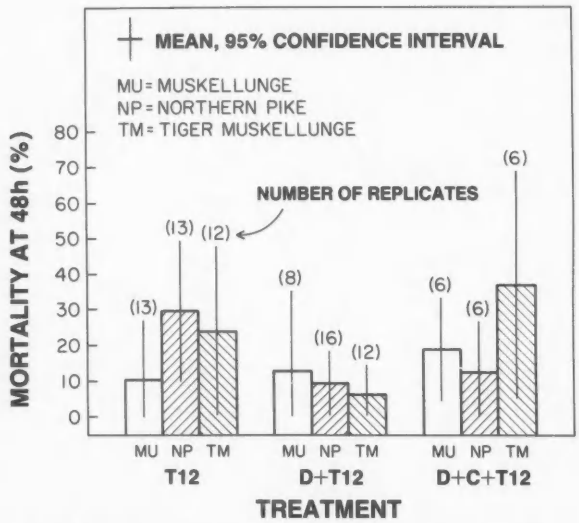


FIG. 2. Mean mortality at 48 h of 15°C acclimated young-of-year muskellunge (MU), northern pike (NP), and tiger muskellunge (TM) subjected to multiple stressors. A 12° temperature increase, T12, is presented first for comparison. The second treatment, D + T12, included a 30-s dipnet handling (D) followed by a 12° rapid temperature increase (T12). The third treatment, D + C + T12, combined a 30-s dipnet (D) followed by 120-min high-density confinement (C) (60 g·L$^{-1}$) with a 12° rapid temperature increase (T12). In every case, temperature was increased at a rate of 1.60°·min$^{-1}$.

Mortalities of all three esocids held in cages after five routine field stockings were low. No mortality occurred when lake temperatures were ≤25°C whereas some mortality (0.0–6.6%) occurred when lake temperatures were >25°C (Table 1). Mortality did not differ among the two species and their hybrid even though mortality varied across years.

## Discussion

We found no differences in survival among muskellunge, northern pike, and their hybrid, the tiger muskellunge, in response to thermal stressors. These results are consistent with other evaluations of response to extreme temperature among related taxa. Lee and Rinne (1980) found no differences in critical thermal maxima of five closely related trout species. Bidgood and Berst (1969) could not distinguish among four stocks of rainbow trout (*Salmo gairdneri*) using upper lethal temperatures. Bevelhimer et al. (1985) found no differences in metabolic rate among the three esocids used in our study.

Unlike previous studies, we did not find any evidence that hybrids survive extreme temperatures better than their parents. Previous studies have found that juvenile and larval tiger muskellunge (Scott 1964; Bonin and Spotila 1978) and carp hybrids (Bettoli et al. 1985) survived extreme temperatures better than the parent species. For example, Scott (1964) found that juvenile tiger muskellunge, acclimated to 25°C, survived 33.0°C with a resistence time of 400 min, but muskellunge and northern pike survived only 32.5°C. The maximum differences between hybrid and parent (i.e. between the highest temperature survived by the hybrid and the highest temperature survived by the least tolerant parent species) in the above three studies are 0.5° (Scott 1964) and 1.2° (Bonin and Spotila 1978) for esocids and 1.5° (Bettoli et al. 1985) for carp. While statistically significant, the magnitude of these increased hybrid tolerances to high temperature is small compared with the magnitude of naturally occurring temperature fluctuations. We chose our experimental method because, unlike the upper lethal temperature and critical thermal maximum used by the investigators discussed above, our method produces results that are ecologically meaningful, readily interpretable, and immediately applicable to fisheries biologists.

The ability of closely related fish to survive extreme temperatures reflects geographic distribution for some species (Brett 1952; Cichra et al. 1982). Muskellunge are distributed more southerly than northern pike (Crossman 1978) and thus might both survive better and grow faster at high temperatures than northern pike. Because we used *E. masquinongy ohioensis*, the most southerly distributed subspecies of muskellunge (Trautman 1981; Koppelman and Philipp 1986), we expected any difference caused by geographic range to be exacerbated. In our work, ability to survive high temperature did not reflect this geographic distribution. Bevelhimer et al. (1985) hypothesized that the Ohio parental stock of northern pike may have become adapted to warmer Ohio waters. If true, this could increase the upper temperature limits for survival in northern pike and could contribute to the lack of differences among the two species. We found no evidence of a differential ability to survive extreme temperatures among esocids based on native geographic distribution, but additional comparisons of thermal adaptation among stocks of both northern pike and muskellunge are required.

Reducing the rate of temperature increase from 1.60 to $0.15°\cdot min^{-1}$ did not reduce mortality for fish exposed to a 15° temperature increase. Whereas tempering may prolong time of death, our data suggest that beyond a critical temperature, 30°C for 15°C acclimated fish, reducing the rate of temperature increase does not appreciably increase survival. Neither handling nor confinement at densities encountered during stocking increased mortality if fish survived the rapid temperature increase. Mather et al. (1986) also demonstrated that thermal stress was the most important cause of poststocking mortality in young-of-year tiger muskellunge. In contrast, even without thermal stress, handling and confinement caused significant mortality in freshwater drum (*Aplodinotus grunniens*) (Johnson and Metcalf 1982) and largemouth bass (*Micropterus salmoides*) (Carmichael et al. 1984). Esocids reared in hatcheries may be less susceptible to handling and crowding than other fish. Species, size, nutritional condition, duration of handling, duration of confinement, density of confinement, water quality during transport, and additives during transport all influence poststocking mortality (Mather et al. 1986).

Field stocking confirmed our finding that thermal stress influences esocid mortality. No mortality occurred when lake temperatures were ≤25°C and some mortality occurred when temperatures exceeded 25°C. Discrepancies between the critical temperature (25 vs. 27°C) causing mortality in the laboratory and field probably resulted from different acclimation temperatures in laboratory (15°C) and field (20°C). Poststocking mortalities of young-of-year tiger muskellunge approached 30% when thermal stresss was ≥10°C (Stein et al. 1981; Carline et al. 1986), supporting our conclusion that thermal stress is an important cause of poststocking mortality.

Because all three esocids responded similarly to handling, confinement, and thermal stressors, differential susceptibility to stocking stress need not be considered when deciding which esocid to stock. Because mortality is a variable response and untested multiple stressors may reduce ability to survive high temperatures, acceptable temperature increases at stocking should be conservative. Healthy fish acclimated to 15°C, experiencing temperature increases ≤10°, should suffer little stress-related mortality.

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# Lack of Response of Channel Catfish (*Ictalurus punctatus*) to Dietary Myo-inositol

G. J. Burtle[1] and R. T. Lovell

*Department of Fisheries and Allied Aquaculture, Auburn University, AL 36849, USA*

Burtle, G. J., and R. T. Lovell. 1989. Lack of response of channel catfish (*Ictalurus punctatus*) to dietary myo-inositol. Can. J. Fish. Aquat. Sci. 46: 218–222.

Channel catfish (*Ictalurus punctatus*) fingerlings were fed for 28 wk in aquaria (28 ± 1°C) on semipurified diets with supplemental myo-inositol (400 mg·kg diet$^{-1}$), without myo-inositol, and without myo-inositol but with succinylsulfathiazole to suppress intestinal bacteria synthesis. Omission of myo-inositol from the diet, with or without the antibiotic, did not reduce growth rate, produce overt signs of myo-inositol deficiency, or cause a decrease in tissue (muscle, liver, and brain) concentration of myo-inositol. No lipid accumulation occurred in liver or kidney when myo-inositol was deleted from the diet. The only possible lipotropic effect of myo-inositol deficiency was a slightly higher ($P < 0.07$) amount of lipid in brain tissue. Myo-inositol synthesis by enzymes in liver and brain tissues was not affected by myo-inositol in the diet. Rates of myo-inositol synthesis were 39.8 and 67.3 μmol·h$^{-1}$·g protein$^{-1}$ for liver and brain, which are higher than synthesis rates reported in rodents (myo-inositol synthesis has not been measured in other fish). This study showed that de novo synthesis of myo-inositol by fingerling channel catfish was sufficient for normal growth and maintenance of tissue levels of myo-inositol and to prevent overt signs of myo-inositol deficiency when the vitamin was not included in the diet.

Des barbues de rivière (*Ictalurus punctatus* de l'année gardées en aquarium (28 ± 1°C) ont été nourries pendant 28 sem d'aliments semi-purifiés enrichis au myo-inositol (400 mg·kg de nourriture$^{-1}$), d'aliments sans myo-inositol et d'aliments sans myo-inositol mais contenant du succinylsulfathiazole, un antibiotique supprimant la synthèse bactérienne intestinale. L'omission du myo-inositol, avec ou sans antibiothique, n'a ni abaissé le taux de croissance, ni déterminé l'apparition de signes manifestes d'une insuffisance en myo-iositol, ni entraîné une baisse de la concentration de myo-inositol dans les tissus (muscles, foi et cerveau). Lorsque le myo-inositol a été reitré de la ration alimentaire, il ne s'est pas accumulé de lipides dans le foi ou dans les reins. La présence d'une quantité de lipides légèrement plus élevée ($P$ inf. à 0,07) dans les tissus cérébraux est le seul effet lipotrope possible de la carence en myo-inositol. Le myo-inositol alimentaire n'a pas influé sur la synthèse enzymatique de ce composé dans les tissus du foi et du cerveau où elle se fait respectivement au rythme de 39,8 et 67,3 μmoles·h$^{-1}$·g$^{-1}$ de protéine, ce qui est plus élevé que les vitesses de synthèses mesurées chez les rongeurs (la synthèse de myo-inositol n'a pas été mesurée chez d'autre poissons). Cette étude montre que la synthèse de novo de myo-inositol chez la barbue de rivière de l'année est suffisante pour que la croissance du poisson et la concentration de myo-inositol tissulaire soient normales et pour prévenir l'apparition de signes manifestes d'une carence en myo-inositol lorsque cette vitamine est absente du régime alimentaire.

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Myo-inositol (inositol) is a structural component of living tissues and occurs as a phospholipid (lipositol) in animal cells. A dietary deficiency has been demonstrated in common carp (*Cyprinus carpio*), red sea bream (*Chrysophrys major*), Japanese eel (*Anguilla japonica*), rainbow trout (*Salmo gairdneri*), chinook salmon (*Oncorhynchus tshawytscha*), and shrimp (*Penaeus japonicus*) (McTaren et al. 1947; Halver 1957; Aoe and Masuda 1967; Yone et al. 1971; Arai et al. 1972; Deshimaru and Kuroki 1976). Myo-inositol deficiency signs common among these species include poor growth, anorexia, and fin and skin lesions. In addition, white–grey intestine was found in eel (Arai et al. 1972), reduced molting occurred in shrimp (Deshimaru and Kuroki 1976), and slow gastric emptying, reduced cholinesterase and transaminase activities, and decreased levels of tissue phosphotides were observed in rainbow trout (McTaren et al. 1947). However, channel catfish (*Ictalurus punctatus*) (Dupree 1966) and Japanese ayu (H. Aoe, Nisshin Flour Milling Co., Ltd., Central Research Laboratory, 177 Tsurugaolsa, Ohi-mashi, Iruma, Saitoma, 354 Japan, pers. comm.) did not demonstrate overt deficiency signs when fed myo-inositol deficient diets.

Dietary levels of carbohydrates (Yone et al. 1971; Kuksis and Mookerjea 1978) and lipids (Kuksis and Mookerjea 1978; Chu and Geyer 1983) appear to influence the severity of myo-inositol deficiency. Feeding myo-inositol-deficient diets to rodents causes fat accumulation in liver, kidney, or intestine (Handler 1946; Hayashi et al. 1974; Chu and Geyer 1981). Suppression of intestinal bacteria growth produced hepatic lipid accumulation in rats that was prevented by adding inositol to the diet (Nielsen and Black 1944), suggesting that intestinal synthesis may be a source of myo-inositol for some species.

Myo-inositol has not been established as an essential nutrient in most warm-blooded animals, including humans; however,

[1]Present address: Georgia Agricultural Experiment Station, Tifton, GA 31793, USA.

TABLE 1. Percentage composition of basal, carbohydrate-free, and lipid-free diets to which myo-inositol or antibiotic were added to replace cellulose.

| Item | Basal | Carbohydrate-free | Lipid-free |
|---|---|---|---|
| Ingredients | | | |
| Vitamin-free casein | 42 | 42 | 42 |
| Dextrin | 23 | 0 | 45.5 |
| Soybean oil | 4 | 11.2 | 0 |
| Cod-liver oil[a] | 3 | 3 | 0 |
| Cellulose | 19.65 | 35.45 | 4.15 |
| Carboxymethylcellulose | 3 | 3 | 3 |
| Mineral mix[b] | 4 | 4 | 4 |
| Myo-inositol-free vitamin mix[c] | 1.35 | 1.35 | 1.35 |
| Diet characteristics | | | |
| Protein (%) | 40 | 40 | 40 |
| Digestible energy (kcal·g$^{-1}$) | 2.8 | 2.8 | 2.8 |

[a]Contained 850 IU vitamin A·g$^{-1}$ and 85 IU vitamin D·g$^{-1}$.

[b]Mineral mixture of Williams and Briggs (1963) supplemented (mg·kg diet$^{-1}$) with cobalt chloride, 1; aluminum potassium sulfate, 0.7; and sodium selenite, 0.8.

[c]Provided the following diluted in cellulose (mg·kg diet$^{-1}$): thiamin, 20; choline chloride, 2000; niacin, 150; riboflavin, 20; pyridoxine, 20; folic acid, 5; calcium pantothenate, 200; vitamin $B_{12}$, 0.06; retinyl acetate (500 000 IU·g$^{-1}$), 8; alpha-tocopherol, 50; cholecalciferol (1 000 000 IU·g$^{-1}$), 2; menadione sodium bisulfite, 10; biotin, 1; *l*-ascorbic acid, 100; ethoxyquin (an antioxidant), 200.

myo-inositol deficiency has been produced in rodents (mice, rats, and gerbils) (Kuksis and Mookerjea 1978). Essentiality of dietary inositol for various species is generally considered to be dependent upon the rate of activity of two enzymes necessary for myo-inositol synthesis, L-myo-inositol-1-phosphate synthetase (EC 5.5.1.4) and L-myo-inositol-1-phosphatase (EC 3.1.3.25) (Eisenberg 1967).

Because dietary myo-inositol is essential for several fish and shellfish species, and intensive feeding of channel catfish for food is commercially important, a reevaluation of the dietary requirement of myo-inositol seemed necessary. We studied channel catfish fingerlings fed semipurified diets with and without supplemental myo-inositol to demonstrate dietary dependence of the fish for myo-inositol. Rates of myo-inositol synthesis by brain and liver tissues of the fish were measured.

## Methods

Full-sibling channel catfish fingerlings (average weight 5.1 g) of the Auburn strain were fed nine isocaloric semipurified diets in triplicate 40-L aquaria containing 25 fish each for 28 wk. Three factors, myo-inositol (400 mg·kg$^{-1}$), no myo-inositol, and no myo-inositol plus an antibiotic succinylsulfathiazole (1%), were each varied in a basal, a carbohydrate-free, and a lipid-free diet (Table 1). The antibiotic, added to suppress intestinal synthesis of myo-inositol, replaced 1% cellulose in the diet. Charcoal-filtered city water flowed through the aquaria at a rate of 1 L·min$^{-1}$ and was maintained at 30 ± 1°C. The diets were fed at the rate of 3% (dry basis) of fish weight daily which is near satiation for small channel catfish. Uneaten food and feces were removed from the aquaria 1 h after feeding. Insides of the aquaria were scrubbed approximately three times weekly to prevent algal or fungal growth which might be a source of nutrients for the fish. The diets were prepared by mixing the ingredients, adding 35% water, and extruding through a 1.6-mm plate with a food grinder. The extruded strands were broken into 5-mm lengths and frozen until 24 h before feeding. Feeding was adjusted weekly subsequent to weighing of the fish.

TABLE 2. Average weight gain per fish for channel catfish fed basal, lipid-free, and carbohydrate-free diets with myo-inositol, without myo-inositol, and without myo-inositol but with supplemental antibiotic (succinylsulfathiazole). Data are means ± SEM for three replicates of 25 fish. Means followed by the same letter are not different at $P < 0.05$.

| Diet | Initial weight (g) | Weight gain (g) |
|---|---|---|
| Basal | | |
| + myo-inositol | 5.0 | 36.4 ± 2.27 a |
| − myo-inositol | 4.8 | 35.6 ± 1.91 a |
| − myo-inositol + antibiotic | 4.8 | 34.0 ± 2.51 a |
| Lipid-free | | |
| + myo-inositol | 5.0 | 20.2 ± 1.41 b |
| − myo-inositol | 5.2 | 16.6 ± 1.21 b |
| − myo-inositol + antibiotic | 4.8 | 17.4 ± 2.01 b |
| Carbohydrate-free | | |
| + myo-inositol | 5.0 | 16.5 ± 1.01 b |
| − myo-inositol | 4.9 | 20.2 ± 1.21 b |
| − myo-inositol + antibiotic | 4.7 | 18.8 ± 1.71 b |

The basal diet was tested for the presence of myo-inositol by extracting with HCl and $NaSO_4$ (de Boland et al. 1975) and measuring any extracted inositol colorimetrically (Lornitzo 1968). The myo-inositol content was less than 10 mg·kg$^{-1}$ which was considered inconsequential in comparison with the dietary inositol requirements of carp (Aoe and Masuda 1967) and rainbow trout (Halver 1982) which are over 400 mg·kg$^{-1}$.

At the end of the experiment, after the fish were weighed, fish were collected from each treatment for hematocrit determination, lipid and myo-inositol analysis of selected tissues, and enzyme assay of brain and liver. Hematocrits and enzyme activity were measured in fresh fish and the other analyses were done with frozen tissues (−87°C).

### Hematocrit, Lipid Analysis, and Myo-inositol Determination

Hematocrits were determined for six fish per treatment using the method of Sniezko (1960). Lipid content of liver, muscle, and kidney for four fish per treatment was determined by chloroform–methanol extraction (Folch et al. 1957). Moisture was determined after drying for 6 h at 100°C. Myo-inositol was extracted from liver and brain tissues of four fish per treatment with boiling water as described by Platt and Glock (1943) and assayed by the colorimetric procedure described by Lornitzo (1968).

### Enzyme Assay

Liver and brain tissue from six fish per treatment were homogenized for 3 min in 10 mL of 0.02 M phosphate buffer containing $5 \times 10^{-4}$ M glutathione in an ice bath. The homogenate was heated (60°C) for 2 min to destroy glucose-6-phosphatase and then diluted with 10 mL of phosphate buffer and centrifuged for 10 min at 900 × *g*. The supernatant was further centrifuged at 45 000 × *g* at 2°C for 2.25 h. The final supernatant was dialyzed against 0.005 M tris-chloride buffer, pH 7.2, at 2°C. Assay for the conversion of glucose-6-phosphate to myo-inositol by enzymes in the tissue extracts (myo-inositol-

TABLE 3. Effect of experimental diets on free myo-inositol concentration (μmol·g dry tissue$^{-1}$) in liver and brain of channel catfish. Data are means ± SEM for four fish per treatment. There was no difference among treatment means within liver or within brain ($P > 0.05$); there was a difference in mean concentration between liver and brain ($P < 0.01$).

| Diet | Liver | Brain |
|---|---|---|
| Basal | | |
| + myo-inositol | 1.90 ± 0.127 | 4.75 ± 0.187 |
| − myo-inositol | 1.87 ± 0.099 | 4.40 ± 0.086 |
| − myo-inositol + antibiotic | 1.63 ± 0.159 | 4.38 ± 0.034 |
| Lipid-free | | |
| + myo-inositol | 1.82 ± 0.204 | 4.82 ± 0.282 |
| − myo-inositol | 1.79 ± 0.270 | 4.47 ± 0.383 |
| − myo-inositol + antibiotic | 1.72 ± 0.257 | 4.60 ± 0.221 |
| Carbohydrate-free | | |
| + myo-inositol | 1.71 ± 0.189 | 4.79 ± 0.443 |
| − myo-inositol | 1.70 ± 0.114 | 4.63 ± 0.234 |
| − myo-inositol + antibiotic | 1.91 ± 0.289 | 4.39 ± 0.213 |

TABLE 4. Effect of experimental diets on myo-inositol synthetase activity (μmol myo-inositol synthesized·h$^{-1}$·g protein extract$^{-1}$) in channel catfish liver and brain.[1] Data are means ± SEM for 10 fish per treatment. Means followed by the same letter are not diferent at $P < 0.05$.

| Diet | Liver | Brain |
|---|---|---|
| Basal | | |
| + myo-inositol | 39 ± 3.5 a | 67 ± 6.8 a |
| − myo-inositol | 46 ± 2.4 b | 58 ± 5.1 a |
| − myo-inositol + antibiotic | 44 ± 3.0 b | 54 ± 6.3 a |
| Lipid-free | | |
| + myo-inositol | 40 ± 3.2 a | 58 ± 4.7 a |
| − myo-inositol | 41 ± 3.8 a | 65 ± 6.3 a |
| − myo-inositol + antibiotic | 39 ± 2.8 a | 63 ± 5.4 a |
| Carbohydrate-free | | |
| + myo-inositol | 41 ± 3.9 a | 63 ± 4.2 a |
| − myo-inositol | 41 ± 2.3 a | 61 ± 2.9 a |
| − myo-inositol + antibiotic | 40 ± 3.3 a | 60 ± 6.3 a |

1-phosphate synthase and inositol-1-phosphatase) followed the colorimetric procedure of Charalampous and Chen (1966). Protein in the extracts was determined by the biuret method. Free myo-inositol produced after 1 h of incubation was assayed spectrophotometrically at 450 μ in protein- and sugar-free filtrates (Charalampous and Chen 1966).

### Statistical Analysis

Analysis of variance (Steel and Torrie 1960) was used to test for a difference among treatments. Treatment means were compared by Duncan's new multiple range test (Duncan 1955).

## Results

### Growth and Overt Deficiency Signs

The omission of supplemental dietary myo-inositol, with or without the addition of succinylsulfathiazole, did not suppress weight gains by fish fed the basal, lipid-free, or carbohydrate-free diets. However, reduction in weight gain was caused by the dietary extremes of no carbohydrate and no lipid (Table 2). No gross anomalies that could be attributed to myo-inositol deficiency were observed by examination of external and internal tissues.

### Tissue Concentration of Myo-inositol

No significant differences in myo-inositol content in a given tissue were found among treatments. The myo-inositol content of brain tissue was higher than that in liver tissue (Table 3). Brain myo-inositol content averaged 4.51 μmol·g$^{-1}$ and liver myo-inositol content averaged 1.80 μmol·g$^{-1}$. These values compare with 0.82 μmol·g$^{-1}$ in the liver of sockeye salmon (*Oncorhynchus nerka*) (Tsuyuki and Idler 1960), 2.66 μmol·g$^{-1}$ in the hepatopancreas of common carp (*Cyprinus carpio*) (Aoe and Masuda 1967), and 5.99 μmol·g$^{-1}$ in the brain of rats (Wells et al. 1965).

### Tissue Synthesis of Myo-inositol

The liver and brain tissues showed high levels of myo-inositol synthesis activity (combined activities of myo-inositol-1-phosphate synthase and inositol-1-phosphatase) (Table 4). Myo-inositol synthesis for catfish brain and liver averaged, respectively, 67.3 and 39.8 units of activity (micromoles per hour per gram of protein) when myo-inositol was present in diets containing both lipid and carbohydrate. Under similar in vitro conditions, a yeast inositol synthetase system had 29 units of activity and that in rat testes had 13 units of activity (Chen and Charalampous 1965). There was no difference in myo-inositol synthesis activity among the nine treatments for brain tissue ($P > 0.05$). Enzyme activity in liver was higher ($P < 0.05$) when the diet contained both lipid and carbohydrate and no supplemental myo-inositol.

### Hematocrits and Tissue Lipid Contents

Hematocrit was not affected by any dietary treatment ($P > 0.05$). The mean hematocrit for the fish in this study was 36.4 ± 2.69%.

Lipid contents of liver and kidney were not different among the diets ($P > 0.05$) (Table 5). Average liver lipid was 11.6% and average kidney lipid was 44.4% (dry basis). Brain lipid was slightly lower ($P < 0.07$) in fish fed diets containing supplemental myo-inositol (22.8%) than in fish fed the myo-inositol-deficient diets (35.7%).

## Discussion

Over a long-term feeding period (28 wk) the channel catfish fed myo-inositol-deficient diets grew normally, did not show overt deficiency signs reported in other fish species (McTaren et al. 1947; Halver 1957; Aoe and Masuda 1967; Yone et al. 1971; Arai et al. 1972; Deshimaru and Kuroki 1976), and maintained tissue levels of free myo-inositol. Adding antibiotic to myo-inositol-deficient diets did not affect the measured responses in the fish, indicating that intestinal microflora were not an important source of inositol synthesis. Tissue synthesis of myo-inositol appears to be sufficient to meet the needs of channel catfish fingerlings for normal growth and health. Metabolic synthesis of myo-inositol probably occurs in liver, kidney, testes, and other tissues of most animals (Kuksis and Mookerjea 1978), but rate of synthesis, as well as physiological and nutritional stresses, determines dietary dependency by the animal for myo-inositol (Chu and Geyer 1983). Rate of liver synthesis in the channel catfish was higher than that in rats

TABLE 5. Percentage lipid concentration in liver, kidney, and brain of channel catfish. Data are means ± SEM for four fish per treatment. Means followed by the same letter are not different at $P < 0.07$.

| Diet | Liver | Kidney | Brain |
|---|---|---|---|
| Basal | | | |
| + myo-inositol | 9.5 ± 2.8 a | 39.1 ± 3.4 a | 18.1 ± 0.9 a |
| − myo-inositol | 9.4 ± 1.0 a | 43.1 ± 6.2 a | 25.3 ± 2.0 ab |
| − myo-inositol + antibiotic | 8.8 ± 1.6 a | 43.7 ± 5.4 a | 37.4 ± 10.4 c |
| Lipid-free | | | |
| + myo-inositol | 12.7 ± 3.8 a | 36.6 ± 4.6 a | 22.5 ± 2.5 a |
| − myo-inositol | 8.7 ± 3.4 a | 49.6 ± 8.8 a | 35.1 ± 2.6 b |
| − myo-inositol + antibiotic | 9.0 ± 2.4 a | 45.0 ± 7.8 a | 53.6 ± 6.35 c |
| Carbohydrate-free | | | |
| + myo-inositol | 13.6 ± 1.6 a | 54.3 ± 3.7 a | 27.0 ± 3.6 ab |
| − myo-inositol | 20.1 ± 5.2 a | 44.3 ± 6.7 a | 32.9 ± 6.8 b |
| − myo-inositol + antibiotic | 12.3 ± 3.3 a | 43.9 ± 7.5 a | 30.0 ± 4.8 b |

(Chen and Charalampous 1965) and gerbils (Chu and Geyer 1983).

The only possible indication of a dietary need for myo-inositol by channel catfish was the slightly but not significantly ($P < 0.07$) higher lipid content of brain tissue in the fish deprived of dietary myo-inositol. The brain tissue contained higher concentrations of myo-inositol than the liver, indicating that brain tissue may require more myo-inositol for normal function than other tissues and thus be more sensitive to a dietary deficiency of myo-inositol. However, the concentration of myo-inositol in the brain tissue was not affected by the omission of myo-inositol from the diet.

Amount and source of carbohydrate and lipid affect myo-inositol requirement in some species (Kroes et al. 1973; Chu and Geyer 1983). Our study showed that altering levels of carbohydrate (dextrin) or lipid (soybean and fish oils) influenced weight gain of channel catfish but did not affect their need for a dietary source of myo-inositol.

Dietary dependence for myo-inositol apparently varies among fishes. Dupree (1966) was unable to demonstrate an inositol deficiency in channel catfish after 30 wk, and H. Aoe (pers. comm.) could not produce a myo-inositol deficiency in ayu. Dietary requirements for myo-inositol-dependent species are high; 400 mg·kg diet$^{-1}$ is recommended for salmonids (Halver 1982) and 440 mg·kg$^{-1}$ is recommended for common carp (Aoe and Masuda 1967). The species which require myo-inositol may have a lower rate of tissue synthesis than those which do not. We conclude from our study that under normal growing conditions, channel catfish 5 g and above all grow and function normally without a dietary source of myo-inositol. However, we reserve the possibility that environmental or nutritional stresses may be created that can produce a dietary requirement for myo-inositol by this fish.

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# Relationships among Tubificid Abundances, Sediment Composition, and Accumulation Rates in Lake Erie[1]

J. A. Robbins

*Great Lakes Environmental Research Laboratory, NOAA, 2205 Commonwealth Blvd., Ann Arbor, MI 48104, USA*

T. Keilty, D. S. White

*School of Natural Resources, University of Michigan, Ann Arbor, MI 48104, USA*

and D. N. Edgington

*Center for Great Lakes Studies, University of Wisconsin-Milwaukee, Milwaukee, WI 53201, USA*

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Sediment cores taken at 15 sites within the three main depositional basins of Lake Erie from 1976 to 1982 were sectioned in 1-cm intervals and analyzed for the abundance and vertical distribution of benthic organisms, $^{137}Cs$, and $^{210}Pb$ (in some cores) and for surficial (upper 2 cm) organic and inorganic carbon. Zoobenthos populations were dominated (>85%) by tubificids (*Limnodrilus hoffmeisteri*, *Quistadrilus multisetosus*, and *Tubifex tubifex*) and varied in abundance from 6600 to 55 300 individuals·m$^{-2}$. The depth above which 90% of the individuals occurred correlated significantly with their abundance and with radiometrically determined mixed depths. Rates of sediment reworking by tubificids exceeded sedimentation rates by 5–80 times, indicating that worms alone can produce the observed zone of constant tracer activity at the sediment–water interface. Tubificid abundance was not significantly related to organic carbon but instead correlated strongly with the sediment accumulation rate and organic carbon flux. In Lake Erie the abundance of tubificids may be limited by the rate of supply of nutrients as measured roughly in terms of the organic carbon flux.

On a prélevé des carottes de sédiments en 15 points des trois principaux bassins de sédimentation du lac Érié de 1976–82; après les avoir divisées en rondelles de 1 cm d'épaisseur, on les a analysées pour connaître l'abondance et la distribution verticale des organismes benthiques ainsi que du $^{137}Cs$ et du $^{210}Pb$ (dans certaines des carottes), et doser le carbone organique et inorganique dans la couche superficielle (deux premiers centimètres). On a constaté que les populations zoobenthiques se composent surtout (plus de 85 %) de tubificidés (*Limnodrilus hoffmeisteri*, *Quistadrilus multisetosus* et *Tubifex tubifex*) et que leur densité varie de 6,600 à 55,300 individus par ·m$^2$. Il y a une corrélation significative entre la profondeur au-dessus de laquelle se trouvent 90 % des individus et l'abondance de ces derniers d'une part, et, d'autre part, le profil radiométrique des profondeurs variées. La vitesse à laquelle les sédiments sont retravaillés par les tubificidés dépasse de 5 – 80 fois la vitesse de sédimentation, ce qui signifie qu'à eux seuls les vers peuvent avoir produit la zone où l'on a observé que l'activité du traceur était constante à l'interface sédiments–eau. L'abondance des tubificidés n'a pu être reliée d'une manière significative au carbone organique, mais on a noté par contre qu'elle était en corrélation marquée avec l'accumulation de sédiments et le flux de carbone organique. Il se peut que dans le lac Érié l'abondance des tubificidés soit limitée par l'apport de matières nutritives, facteur évalué approximativement d'après le flux de carbone organique.

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Tubificid worms are often the dominant members of the benthic community in the Great Lakes, with abundances in excess of 200 000 individuals·m$^{-2}$ (Brinkhurst 1970). The feeding action of these and other oligochaetes significantly alters radionuclide and contaminant profiles and contributes to the persistence of such constituents in the water column (Robbins et al. 1977, 1979; Robbins 1982; Eadie and Robbins 1987). Studies such as those of Robbins et al. (1977) and Fisher et al. (1980) have shown that in general the numbers of oligochaetes are sufficient to homogenize near-surface sediments. In Lake Erie the rate of sediment turnover by oligochaetes can exceed the sedimentation rate by more than an order of magnitude (Fisher et al. 1980). Thus, sediments can usually be cycled through the gut of such organisms many times before burial.

The primary food source of tubificids is thought to be particular bacteria (Brinkhurst and Chua 1969; Wavre and Brinkhurst 1971; Brinkhurst et al. 1972; Monikov 1972; Brinkhurst 1974; McMurtry et al. 1983). Because bacterial populations are associated with organic portions of sediments (Dutka et al. 1974), abundance and species composition have correlated with levels of organic enrichment in some cases (Brinkhurst 1969; Mozley and Howmiller 1977; Howmiller and Scott 1977). Brinkhurst and Austin (1979) showed that, in fact, worms selec-

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tively feed on organically rich sediment. Despite this, there are many instances where tubificid worm abundances have not correlated well with the organic carbon content of sediments (Della Groce 1955; Pliodzinskas 1978; McMurtry et al. 1983; Lauritsen et al. 1985). Poor correlations can occur if reworking redistributes and dilutes food resources or if increased sedimentation of inert materials suppresses the concentration of organic carbon but has little effect on the ability of the organisms to make use of it.

The present study was undertaken to determine if the abundance of tubificids in pelagic sediments of the Great Lakes was correlated with either the amount of organic material or its rate of supply. A previous study (Robbins 1982) in Lake Huron showed that the depth of sediment mixing was directly related to the organic carbon flux. Other studies in laboratory microcosms (Klahr 1981; White et al. 1987) showed that the depth of tubificid feeding (and mixing) is directly related to their abundance. Such results imply that abundance might be correlated with the organic carbon flux calculated as the product of the mass sedimentation rate and the organic carbon content of near-surface sediments.

Lake Erie provides a suitable environment for examining such relationships. The lake possesses strong horizontal gradients in both sedimentation rates and in the organic carbon content. Sedimentation rates range from zero (or negative in areas of active scouring) to values greater than in any of the other basins in the Great Lakes and have been well determined through seismic (Lewis 1966; Thomas et al. 1976), palynological (Kemp et al. 1977) and radiometric methods (Robbins et al. 1978; Robbins 1982; this study). These alternative methods present a consistent picture of recent sedimentation in the three main basins and show that in the eastern basin, rates can exceed 1 $cm \cdot yr^{-1}$. In addition, because of comparatively high worm abundance in Lake Erie the fractional error in estimating means is significantly less (Downing 1979) than expected in the other more oligotrophic Great Lakes.

## Methods

Sediment cores were collected from Lake Erie in fine-grained sediments along an east–west transect across the three basins (Fig. 1). Sediments at 15 stations were sampled in June 1976. Two additional cores were taken in June 1978 and four more in June 1982 at some of the 1976 sites, making a total of 21 site visits. The sites in the eastern and central basins cover a representative range of sedimentary environments. Cores were taken in duplicate with an open-tube, 6.6-cm-ID Benthos gravity corer equipped with a butterfly valve, hydraulically extruded aboard ship, and sectioned in 1-cm intervals. In 1982, a large box core (50 × 50 × 40 cm depth) was collected in addition to the gravity core at site G16 for purposes of comparison. This site serves as the central basin reference site (CBRS) where sediments have been repeatedly cored during the past 18 yr (see Robbins et al. 1978). A subcore from the box core was obtained by slow insertion of a 6.6-cm-ID core tube. To minimize sediment column distortions in subsampling, we kept the sediment–water interface in the tube aligned with the interface on the outside by making small adjustments in air pressure within the tube during insertion. One set of gravity core sections was preserved by addition of a $CaCO_3$-buffered 10% (v/v) solution of formalin (40%) and water for zoobenthos analysis. The other set and the box subcore used for $^{137}Cs$ ($t_{1/2}$ = 30.1 yr), $^{210}Pb$ ($t_{1/2}$ = 22.3 yr) and carbon analysis were stored frozen aboard ship and subsequently freeze-dried.

Tubificids were separated from sediments using a 0.25-mm sieve. Total numbers were recorded for each 1-cm section. However, species were not identified except in some initial sortings. All identified samples were dominated (approximately 85%) by three species of Tubifcidae, *Limnodrilus hoffmeisteri*, *Quistadrilus multisetosus*, and *Tubifex tubifex*. Other invertebrates occurred in much lower densities: *Asellus racovitzai racovitzai*, *Vejdovskyella intermedia*, *Chaetogaster* sp., *Pisidium* spp., *Sphaerium* spp., *Pontoporeia hoyi*, and Hydracarina.

Cesium-137 measurements were made by methods described in detail elsewhere (Robbins 1980). Freeze-dried material was lightly ground, placed in plastic counting vials of standardized shape, and counted on a system consisting of a lithium-drifted germanium (GeLi) gamma detector coupled to a multichannel analyzer. The system was calibrated by measuring the activity of sediments doped with a precisely known (±2%) amount of the radionuclide. Sedimentation rates were confirmed in some cases by measurement of $^{210}Pb$ as well (Robbins 1978, 1980, 1986a). The activity of $^{210}Pb$ was determined by the alpha spectroscopic methods described in detail elsewhere (Robbins 1980; Flynn 1968). Sedimentation rates and mixed depths were

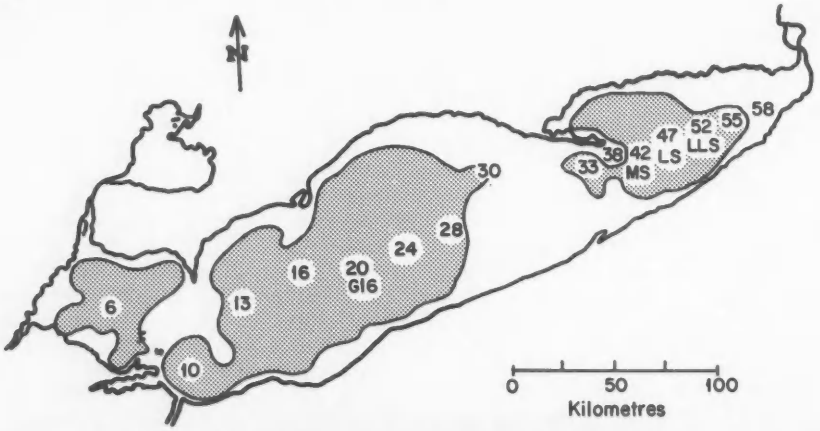


FIG. 1. Principal depositional basins and coring sites in Lake Erie.

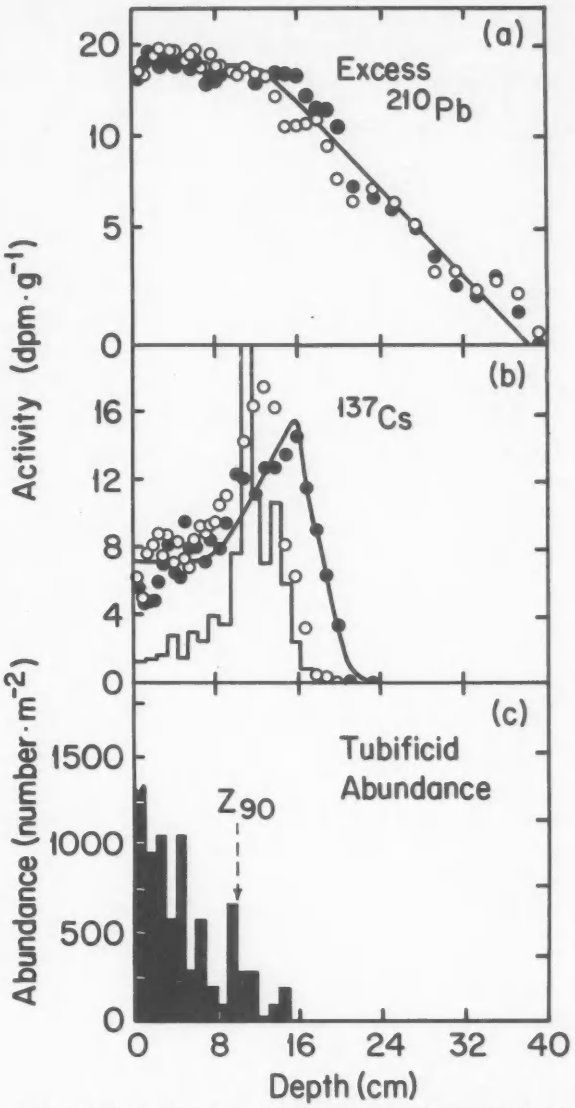


FIG. 2. (a) Distribution of excess $^{210}$Pb in a box core (open circles) and gravity core (solid circles) at site G16 (1982). (b) Distribution of $^{137}$Cs. The solid lines in Fig. 2a and 2b are the RSSM model fitted to the gravity core data. The histogram is the RSSM model $^{137}$Cs distribution expected with no mixing. (c) Number of tubificid worms in each 1-cm interval. Ninety percent of the organisms occur above the indicated depth ($Z_{90}$)

inferred from radionuclide profiles using the rapid steady-state mixing (RSSM) model (Robbins et al. 1977; Robbins 1978; Robbins 1982).

Total and inorganic carbon ($C_i$) were determined by conventional gasometric methods (Kolpack and Bell 1968) using a LECO carbon analyzer. Organic carbon ($C_o$) was calculated as the difference between the total and inorganic carbon content. Values reported are for the upper 2 cm of sediment.

All statistical computations used values of the sedimentation rates, tubificid range ($Z_{90}$), and mixed depths ($Z_m$) based on mass units (grams per square centimetre per year and grams per square centimetre) which eliminate compaction effects. Thus, for example, $Z_{90}$ is the cumulative dry weight of sediment (grams per square centimetre) measured downward from the sediment–water interface within which 90% of the organisms occurred. Regression data were generated via Statistical Applications Software (SAS) programs and the VAX/VMS 780 computing system at the Great Lakes Environment Research Laboratory. Analysis of residuals indicated that assumptions of normality and equal variance were adequately met. Skewness and kurtosis coefficients were confined to the range $-1.0$ to $+1.0$.

## Results and Discussion

### Radionuclide Profiles and Sedimentation Parameters

The distributions of excess $^{210}$Pb and $^{137}$Cs at site G16 (1982) illustrate profiles encountered in the basins and the results of the RSSM model (Fig. 2a, 2b). In the gravity core (solid circles) and box core (open circles) the activity of excess $^{210}$Pb (i.e. background subtracted values) is virtually constant over about the upper 10 cm and decreases exponentially below this depth (Fig. 2a). The solid line is the RSSM model fit to the gravity core data for least-squares optimized values of the mixed depth, 10.3 cm, corresponding to a cumulative dry sediment weight, $Z_m$, of 1.8 g·cm$^{-2}$ and a linear sedimentation rate of 0.63 cm·yr$^{-1}$, corresponding to a mass sedimentation rate, $R$, of 0.11 g·cm$^{-2}$·yr$^{-1}$. Corresponding box core values are 7.3 cm ($Z_m$ = 1.1 g·cm$^{-2}$) and 0.83 cm·yr$^{-1}$ ($R$ = 0.14 g·cm$^{-2}$·yr$^{-1}$). The $^{137}$Cs profiles (Fig. 2B) have pronounced peaks corresponding to the 1963–64 fallout maximum which show a small but systematic displacement from each other. The solid line is the RSSM model fit to the gravity core data for least-squares optimized values of the mixed depth, 8.0 cm ($Z_m$ = 1.2 g·cm$^{-2}$), and sediment accumulation rate, 0.58 cm·yr$^{-1}$ ($R$ = 0.10 g·cm$^{-2}$·yr$^{-1}$). The corresponding RSSM model values for the box core are 6.0 cm ($Z_m$ = 0.9 g·cm$^{-2}$) and 0.52 cm·yr$^{-1}$ ($R$ = 0.085 g·cm$^{-2}$·yr$^{-1}$). The histogram shows the distribution expected in the absence of mixing (i.e. mixed depth set equal to zero in the RSSM model). These results demonstrate the level of consistency in the comparison of RSSM model values based on $^{210}$Pb and $^{137}$Cs in the same core, of the two coring methods, and of serial coring at nominally the same site. For this and other cores in Lake Erie the mixed depth based on $^{210}$Pb is generally somewhat greater than that based on $^{137}$Cs. For a valid comparison of results at different sites, RSSM model values were based on gravity coring and $^{137}$Cs analysis only, since these methods were applied consistently at all locations.

The RSSM model yields sedimentation rates (Table 1) agreeing with previous measures based on seismic and palynological studies (see Robbins et al. 1978). Sedimentation rates are well correlated ($r$ = 0.80, $n$ = 21) with the thickness of postglacial muds as reported by Thomas et al. (1976), indicating that recent deposition patterns and rates reflect long-term accumulation. The $^{210}$Pb data imply that in the central and eastern basins of Lake Erie there has been no discernible change in the rate of sediment accumulation during the past 100 yr (see Eadie and Robbins 1987 for an example at the eastern basin site (LE-81-HS, corresponding to 82-MS). The highest sedimentation rate measured in the present set of cores is over 1.5 cm·yr$^{-1}$ (average in the upper 10 cm), corresponding to a mass sedimentation rate of 0.86 g·cm$^{-2}$·yr$^{-1}$.

TABLE 1. Rapid steady-state mixing model (RSSM) and mixed layer concentration data.

| Site | Sediment accumulation rate ($R$) ($g \cdot cm^{-2} \cdot yr^{-1}$) | Mixed layer mass ($Z_m$) ($g \cdot cm^{-2}$) | Time resolution ($\gamma^{-1}$) (yr) | Flux correction factor | Mixed layer concentration | | |
|---|---|---|---|---|---|---|---|
| | | | | | $^{137}Cs$ ($dpm \cdot g^{-1}$) | Organic carbon (%) | Inorganic carbon (%) |
| 82-G16 | 0.10 | 1.20 | 12 | 1.12 | 7.0 | 3.7 | 0.24 |
| 82-LLS | 0.59 | 3.23 | 5 | 1.05 | 3.5 | 2.6 | 0.55 |
| 82-LS | 0.34 | 1.54 | 4 | 1.04 | 2.6 | 2.3 | 1.10 |
| 82-MS | 0.62 | 2.96 | 5 | 1.05 | 2.0 | 2.2 | 1.24 |
| 78-38 | 0.86 | 5.20 | 6 | 1.06 | 3.5 | 1.6 | 2.59 |
| 78-42 | 0.33 | 2.18 | 7 | 1.07 | 6.7 | 2.2 | 0.95 |
| 76-30 | 0.03 | 0.22 | 7 | 1.07 | 3.1 | 0.8 | 2.53 |
| 76-58 | 0.04 | 0.66 | 17 | 1.16 | 3.6 | 1.7 | 0.47 |
| 76-33 | 0.01 | 0.34 | 34 | 1.34 | 2.2 | 2.0 | 1.73 |
| 76-52 | 0.24 | 0.92 | 4 | 1.04 | 6.7 | 2.7 | 0.41 |
| 76-55 | 0.08 | 0.49 | 6 | 1.06 | 6.3 | 2.4 | 0.48 |
| 76-38 | 0.57 | 3.81 | 7 | 1.07 | 3.5 | 1.7 | 2.25 |
| 76-42 | 0.45 | 1.84 | 4 | 1.04 | 6.7 | 2.4 | 0.81 |
| 76-6 | 0.12 | 1.45 | 12 | 1.12 | 5.8 | 3.0 | 0.39 |
| 76-10 | 0.07 | 1.48 | 21 | 1.21 | 7.0 | 2.5 | 1.10 |
| 76-47 | 0.14 | 0.86 | 6 | 1.06 | 6.7 | 2.6 | 0.63 |
| 76-24 | 0.05 | 0.95 | 19 | 1.19 | 15.8 | 3.6 | 0.42 |
| 76-13 | 0.02 | 0.40 | 24 | 1.24 | 14.2 | 4.3 | 0.33 |
| 76-16 | 0.02 | 0.35 | 18 | 1.18 | 18.8 | 3.5 | 0.23 |
| 76-20 | 0.06 | 0.71 | 12 | 1.12 | 15.9 | 3.5 | 0.04 |
| 76-28 | 0.03 | 0.63 | 21 | 1.21 | 7.3 | 2.0 | 0.69 |

TABLE 2. Carbon fluxes and organism data.

| Site | Organic carbon flux ($F_o$) ($mg\ C \cdot cm^{-2}\ yr^{-1}$) | Mixing-corrected organic carbon flux ($F^*_o$) ($mg\ C \cdot cm^{-2} \cdot yr^{-1}$) | Inorganic carbon flux ($F_i$) ($mg\ C \cdot cm^{-2} \cdot yr^{-1}$) | Tubificid worm abundance ($N$) ($individuals \cdot cm^{-2}$) | Range in mass units ($Z_{90}$) ($g \cdot cm^{-2}$) | Reworking efficiency ($\epsilon$) |
|---|---|---|---|---|---|---|
| 82-G16 | 3.67 | 4.11 | 0.24 | 1.29 | 1.56 | 13 |
| 82-LLS | 15.5 | 16.3 | 3.24 | 3.91 | 3.06 | 7 |
| 82-LS | 8.05 | 8.41 | 3.78 | 3.18 | 4.24 | 9 |
| 82-MS | 13.6 | 14.2 | 7.64 | 3.64 | 3.37 | 6 |
| 78-38 | 13.4 | 14.2 | 22.2 | 4.12 | 3.39 | 5 |
| 78-42 | 7.33 | 7.81 | 3.16 | 2.11 | 2.34 | 6 |
| 76-30 | 0.23 | 0.25 | 0.76 | 1.38 | 3.50 | 46 |
| 76-58 | 0.67 | 0.78 | 0.19 | 1.92 | 0.73 | 48 |
| 76-33 | 0.20 | 0.27 | 0.17 | 0.66 | 0.62 | 66 |
| 76-52 | 6.55 | 6.80 | 0.98 | 4.99 | 0.92 | 21 |
| 76-55 | 1.93 | 2.05 | 0.38 | 2.12 | 1.24 | 27 |
| 76-38 | 9.80 | 10.5 | 12.8 | 5.54 | 4.00 | 10 |
| 76-42 | 10.8 | 11.2 | 3.64 | 4.99 | 3.93 | 11 |
| 76-6 | 3.56 | 3.99 | 0.47 | 2.30 | 3.42 | 19 |
| 76-10 | 1.72 | 2.09 | 0.77 | 0.77 | 2.27 | 11 |
| 76-47 | 3.68 | 3.91 | 0.88 | 2.41 | 0.50 | 17 |
| 76-24 | 1.81 | 2.15 | 0.21 | 1.09 | 0.48 | 22 |
| 76-13 | 0.73 | 0.90 | 0.06 | 1.23 | 0.37 | 72 |
| 76-16 | 0.70 | 0.82 | 0.05 | 1.61 | 0.72 | 81 |
| 76-20 | 2.08 | 2.32 | 0.02 | 2.38 | 0.61 | 40 |
| 76-28 | 0.61 | 0.73 | 0.21 | 1.52 | 0.93 | 51 |

Mixed depths range from 0.2 to 1.2 $g \cdot cm^{-2}$, corresponding to a linear range of 0.5–7 cm in the central basin. In the eastern basin, mixed depths are, on average, three times greater, with a range of 0.34–5.2 $g \cdot cm^{-2}$ corresponding to linear depths from 1 to 10 cm. In both basins, mixed depths generally decrease toward the margins.

## Intensity of Sediment Mixing Processes

The RSSM model is valid only if the rate of sedimentation as well as the rate and range of mixing have remained constant over the period of interest and if the rate is sufficiently high to completely homogenize the mixed layer. This latter assumption has been shown to break down (Eadie and Robins 1987) for tracers such as $^7Be$ ($t_{1/2}$ = 53.4 d) with a sufficiently short half-life. In sediments dominated by conveyor-belt deposit-feeding tubificid worms, a sufficient criterion for complete mixing has been developed based on the subduction rate (Fisher et al. 1980) which is the rate of burial of surface sediments by the pile-up of tubificid fecal material at the sediment interface. Defining the reworking efficiency, $\epsilon$, as the ratio of the subduction rate

(grams per square centimetre per year) to the sedimentation rate (grams per square centimetre per year), it can be shown (Robbins 1986b) that essentially complete mixing occurs for a steady-state distribution of a long-lived tracer such as $^{210}$Pb when $\epsilon > 10$. The efficiency can be calculated for each site from the tubificid abundances (Table 2) and sedimentation rate data, $\epsilon = N\,\Gamma/R$, where $N$ is the mean number of organisms per square centimetre and $\Gamma$ is the mean individual feeding rate. Values of the efficiency (Table 2) are based on an average rate of individual feeding of 1 g·individual$^{-1}$·yr$^{-1}$ (Robbins et al. 1984; Krezoski and Robbins 1985).

With a few exceptions in the eastern basin, the efficiency far exceeds 10, indicating that tubificid worms alone can produce a region of constant $^{210}$Pb activity. A non-steady-state distribution such as that represented by the $^{137}$Cs pulse can be incompletely mixed even for values of $\epsilon > 10$ depending on the time elapsed since its introduction. Incomplete mixing can account for the lower apparent RSSM model mixed depths for $^{137}$Cs than for $^{210}$Pb. The reworking efficiencies increase toward the margins of the main depositional basins and are roughly twice as high in the central basin as in the eastern basin. The present values are generally higher than those previously reported by Fisher et al. (1980).

The value $\gamma^{-1}$ (years) in Table 1 is the ratio of the mixed depth to the sedimentation rate. In terms of the RSSM model, this ratio is the residence time of a particle in the mixed layer and is a measure of core time resolution (Robbins 1980). In Lake Erie as in other Great Lakes (Edgington and Robbins 1976; Robbins 1980) the time resolution increases toward the margins of the basins. In the central basin the average time resolution is about 20 yr (treating site 30 as an "outlier") and in the eastern basin is about 10 yr. These times approximate the characteristic particle-associated traces and contaminant removal times for the process of sedimentation and burial (Robbins 1982). The lowest (best) time resolution reported in Great Lakes profundal sediments, about 5 yr, occurs at centrally located sites in the eastern basin of the lake.

## Vertical Distribution of Tubificids

The vertical distribution of tubificids (Fig. 2c) in the gravity core at site G16 was dominated by high numbers of immature individuals in the uppermost layer (0–1 cm, 6600 individuals·m$^{-2}$). Tubificids occurred in all intervals between 0 and 15 cm but not at depths from 15 to 20 cm. The range at this site was 10.3 cm, corresponding to a cumulative sediment weight, $Z_{90}$, of 1.56 g·cm$^{-2}$. As seen previously (Robbins et al. 1977), tubificids occur primarily within the radiometrically defined mixed layer.

## Carbon Fluxes

The uncorrected organic carbon flux, $F_o$ is calculated as the product of the mass sedimentation rate, $R$ (grams per square centimetre per year), and the organic carbon content, $C_o$ (grams of carbon per gram of dry sediment). This value underestimates the actual flux either if there is significant decomposition of organic carbon or if the flux changes (increases) over time. A consequence of the RSSM model applied to constituents supplied at a constant rate but degrading on burial with first-order kinetics (or radioactive decay) is that the actual flux (mixing-corrected organic carbon flux $F^*_o$) is given by

$$(1)\quad F^*_o = C_o \cdot R \cdot (\gamma + k_o)/\gamma$$

where $k_o$ is the decomposition rate constant (per year). Equation 1 is also correct if the rate of supply increases exponentially with time and $k_o$ is interpreted as the factor in the exponential term describing the increase (Robbins 1980). Therefore the correction does not depend critically on whether the change in the distribution of carbon in a core is due to decomposition or to an exponentially increasing rate of supply. The "rate constant" for either of these processes may be inferred by applying the RSSM model to carbon distributions in dated cores. Avnimelech et al. (1984) have taken this approach (in the limiting case of $Z_m = 0$) for a series of 64 U.S. lakes. Organic carbon distributions have been determined in cores collected in 1971 at three sites in Lake Erie by Kemp et al. (1976) which correspond to ones in this study. Their profiles exhibit a zone at the sediment–water interface of constant organic carbon and a gradual, nearly exponential decrease below this zone. Application of the RSSM model to their data yields the following rate constants: B8 (corresponding to site 76-10), $k_o = 0.007 \cdot \text{yr}^{-1}$; G16 (same designation), $k_o = 0.013 \cdot \text{yr}^{-1}$, and at M32 (same designation), $k_o = 0.010 \cdot \text{yr}^{-1}$. Within experimental error these values are equivalent and yield an average rate constant of $k_o = 0.01 \pm 0.003 \cdot \text{yr}^{-1}$. This value falls in the middle of the range of values reported by Avnimelech et al. (1984). If this rate applies to all sites, the correction is generally small (under 20% for 17 sites, 20–34% for the other four sites). Both uncorrected and corrected fluxes are included in the statistical analysis, since the uncorrected flux is weakly model dependent whereas the corrections to the flux, although estimated to be small, depend strongly on the validity of the RSSM model and the assumption that $k_o$ is site independent. Since inorganic carbon profiles at the above sites show little significant change with depth over the region of interest (Kemp et al. 1976), no correction is applied to the estimate of the inorganic carbon flux, $F_i$.

## Concentrations in the Mixed Layer

The $^{137}$Cs activity (Cs) is well-correlated with the organic carbon content of the mixed layer (Table 3), and as shown previously (Robbins 1980), both constituents along with many other trace constituents are preferentially codeposited with fine-grained, clay-size sediments toward the centers of depositional basins. In contrast, inorganic carbon, which is associated with silt-size dolomitic, terriginous materials (Kemp et al. 1976), is inversely related to both $^{137}$Cs and organic carbon. As in Lake Huron (Robbins 1980, 1987), silt-size sediments are preferentially deposited toward the margins of depositional basins. Concentrations of $^{137}$Cs and organic carbon are inversely (but weakly) related to the sediment accumulation rate, probably as a result of the dilution of transient and autochthonous constituents, respectively. In contrast, inorganic carbon, a terriginous component of bulk sediment, is positively correlated with the sediment accumulation rate.

Tubificid worm abundances in Lake Erie are consistent with previously reported values (McCall and Fisher 1980) and are highest in the eastern basin of the lake where the organic carbon content of near surface sediments is lowest. Abundance ($N$) is not significantly related to either the inorganic or organic carbon ($r = -0.25$, $p = 0.13$) content of the surface sediments (Table 3). Pliodzinskas (1978) also found a weak negative correlation between organic carbon content and tubificid abundance in the offshore western and central basin areas of Lake Erie. Our results are also consistent with the work of McMurtry et al. (1983), who found that sites in Toronto Harbour, Lake

TABLE 3. Correlation coefficients and the level of significance, $P$ (in parentheses). Asterisks indicate that pairs of variables are not independent and correlation coefficients are not reported. Correlations are not considered significant (NS) if $p > 0.10$.

| | $R$ | $Z_m$ | Cs | $C_o$ | $C_i$ | $F_o$ | $F^*_o$ | $F_i$ | $N$ | $Z_{90}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| $R$ | 1 | 0.95 (0.0001) | −0.47 (0.03) | −0.34 (NS) | 0.48 (0.03) | * | * | * | 0.78 (0.0001) | 0.69 (0.0006) |
| $Z_m$ | | 1 | −0.42 (0.06) | −0.31 (NS) | 0.51 (0.02) | 0.87 (0.0001) | 0.87 (0.0001) | 0.91 (0.0001) | 0.66 (0.001) | 0.64 (0.002) |
| Cs | | | 1 | 0.76 (0.0001) | −0.59 (0.005) | −0.45 (0.04) | −0.45 (0.04) | −0.38 (0.09) | −0.34 (NS) | −0.59 (0.005) |
| $C_o$ | | | | 1 | −0.78 (0.0001) | * | * | −0.41 (0.06) | −0.25 (NS) | −0.50 (0.02) |
| $C_i$ | | | | | 1 | 0.30 (NS) | 0.30 (NS) | * | 0.24 (NS) | 0.57 (0.007) |
| $F_o$ | | | | | | 1 | * | * | 0.80 (0.0001) | 0.68 (0.0008) |
| $F^*_o$ | | | | | | | 1 | * | 0.79 (0.0001) | 0.68 (0.0008) |
| $F_i$ | | | | | | | | 1 | 0.60 (0.004) | 0.56 (0.009) |
| $N$ | | | | | | | | | 1 | 0.56 (0.008) |
| $Z_{90}$ | | | | | | | | | | 1 |

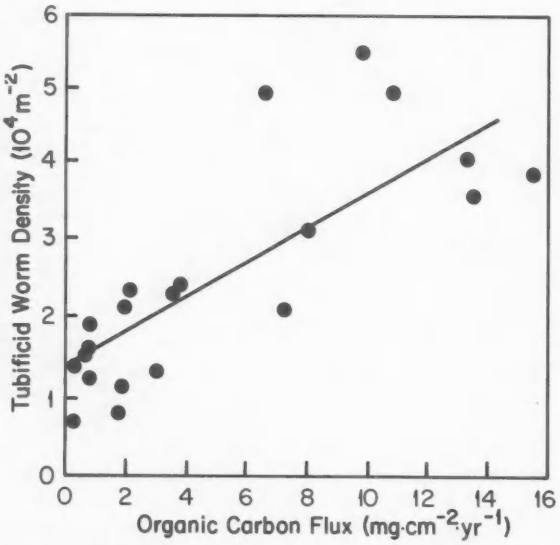


FIG. 3. Relationship between the abundance of tubificid worms and the rate of supply of organic carbon.

Ontario, with lower organic carbon had the higher tubificid abundances. In these cases, worm populations were evidently not limited by low concentrations of a constituent which presumably represents the primary food resource.

Tubificid worm abundances correlate (Table 3; Fig. 3) most highly with sedimentation rate and organic carbon flux. Note that the correlation is slightly higher with $F_o$ than with $R$ despite the fact that the correlation with $C_o$ alone is negative. The mixing correction has very little effect on the value or significance of the correlation (Table 3). The abundance also correlates with $F_i$ primarily because of its strong dependence on $R$. Although the abundance is positively correlated with $C_i$, the effect of forming the product $R$ and $C_i$ ($=F_i$) is to reduce the correlation. These results suggest involvement of organic rather than inorganic carbon in processes affecting the abundance of tubificids.

The above correlations would be expected if the worm abundance is limited by the rate of supply of essential nutrients represented by the organic carbon flux. Evidence for organic carbon as an indicator of food resource in Lake Erie and elsewhere is well established. In Lake Erie, algal remains, which are a primary benthic food source (Anthony and Hayes 1964), settle onto the sediment surface providing organic rich sites for growth of epidetrital bacteria which are related directly to the quantity of the supplied organic carbon (Dutka et al. 1974). However, the total organic carbon content will include not only such constituents as algal remains and bacteria but also humic materials, lignins, and other products which are resistant to decomposition and presumably unavailable as a food resource. For this and other reasons the total organic carbon content is an imperfect measure of the nutrients available to the tubificids.

There is little independent evidence that the rate of nutrient supply is a controlling variable. Keilty et al. (1983) have reported a weak but positive correlation between organic carbon flux and the abundance of the lumbriculid *Stylodrilus heringianus* ($r = 0.51, p = 0.05, n = 25$) and a stronger correlation with total tubificids ($r = 0.74, p = 0.01, n = 31$) in sediments of Lake Michigan. Lang and Hutter (1981) found that oligochaete communities responded differently both qualitatively and quantitatively at two sites in Lake Geneva, Switzerland, with differing fluxes of sedimentary organic carbon (15.7 and 21.4 $mg \cdot cm^{-2} yr^{-1}$. At the site with the higher flux, the absolute and relative abundance of some oligotrophic species such as *Stylodilus heringianus* and *Peloscolex velutinus* decreased by an order of magnitude but the total oligochaete abundance was five times higher.

## Tubificid Range

The range of tubificids is positively correlated with their abundance (Table 3). Previous works have demonstrated that the depth of sediment reworking is directly related to feeding activities and abundance (Davis 1974; Krezoski et al. 1978; McCall and Fisher 1980; Robbins 1982). Both McCall and Fisher (1980) and Klahr (1981) showed that in laboratory microcosms the depth of maximum feeding, $Z_{max}$ (centimetres), was

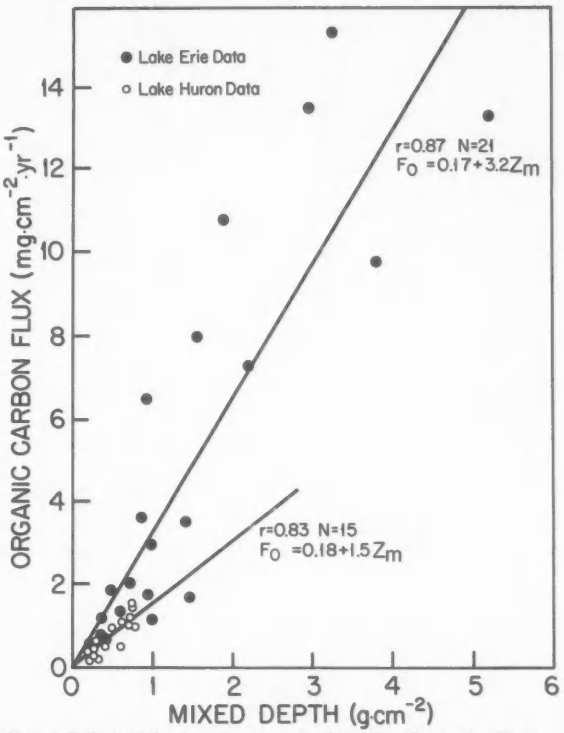


FIG. 4. Relationships between the organic carbon flux and radiometrically determined mixed depth in Lakes Huron (Robbins 1982) and Erie.

related to worm abundance. However, in the laboratory microcosm studies with homogenized sediments, worms appeared to mix materials far less deeply than under in situ conditions. In the study of White et al. (1987) using *Stylodrilus heringianus*, $Z_{max}$ (centimetres) was related to the organism abundance ($N$ in $10^4 \cdot m^{-2}$) by $Z_{max} = 0.04 + 0.33\,N$. In the present study, taking $Z_m$ (centimetres) to represent the maximum depth of feeding, $Z_m = 2.1 + 1.1\,N$. Thus an abundance of $5 \times 10^4 \cdot m^{-2}$ would be associated with about a 2-cm mixed depth in the laboratory study and nearly 8 cm in the field. Such differences could arise for many reasons including the comparison of different worm populations and species, short-term versus long-term measures of sediment mixing, and the breakdown in the relationship between feeding and bacterial distributions in homogenized sediments. Under natural conditions the vertical distribution of bacterial populations has been found to correspond to that of tubificids (Brinkhurst et al. 1969).

The tubificid range also correlated significantly (Table 3) with the RSSM mixed depth, $Z_m$, as expected from the above illustrative example (G16) and the results of several previous studies (Robbins et al. 1977; Robbins 1980, 1982). A comparison of $Z_m$ and $Z_{90}$ in a series of cores from several areas of the Great Lakes by Robbins (1982) yielded an excellent linear relationship: $Z_m$ (centimetres) = 1.2 $Z_{90}$ (centimetres) − 0.3 ($r$ = 0.92, $n$ = 12). The present results are $Z_m$ (cm) = 0.66 $Z_{90}$ + 0.9 ($r$ = 0.70, $n$ = 21). For tubificid ranges greater than a few centimetres, this regression equation predicts a significantly lower RSSM mixed depth than found previously. Reasons for this difference are unclear. However, since the sedimentation rates are generally higher in Erie than at sites in the previous studies, cases of incomplete mixing of $^{137}Cs$ are more often encountered where, as discussed above, the RSSM model underestimates the extent of mixing. This would yield a lower $Z_m$ for most values of $Z_{90}$, as observed. According to the RSSM model the mixed depth is the region of sediment at the interface which is mixed completely (and instantaneously) by all processes redistributing sediment particles. The mixed layer is the time-averaged result of biological (and physical) mixing in which seasonal variations in the abundance of tubificids or fluctuations in their vertical distribution and rates of feeding are averaged over many years. It is therefore remarkable that measurement of the vertical distribution of tubificids ($Z_{90}$) at an instant in time bears any relationship at all to this layer thickness.

The tubificid range is also significantly correlated with the sediment accumulation rate and the fluxes of organic and inorganic carbon (Table 3). Since the range is related to the abundance which in turn is related to the sediment accumulation rate and organic carbon flux, this is an expected result. The correlation with the inorganic carbon flux presumably stems from the association of inorganic carbon with the sedimentation of allochthonous materials as discussed above.

## RSSM Mixed Depth

The correlation between the RSSM mixed depth and the sediment accumulation rate is very high (Table 3). Significant but generally lower correlation coefficients have been reported previously. The earliest observations (Robbins and Edgington 1975), based on limited set of cores from southern Lake Michigan, yielded $r = 0.75$, $n = 7$, with $p = 0.05$. Subsequently, Edgington and Robbins (1976) reported on a larger set of cores from high sedimentation areas of Lake Michigan for which $r = 0.56$, $n = 25$, and $p = 0.003$. However, they also reported on a second set of cores which included many sites on the margins or outside of main depositional basins for which the correlation was poor ($r = 0.28$, $n = 36$, and $p = 0.1$). A set of cores taken within the depositional basins of southern Lake Huron (Robbins 1980) yielded a significant correlation: $r = 0.73$, $n = 60$, and $p = 0.001$. The high correlation in the present case appears to be associated with the location of sites within depositional basins and the wide range of sedimentation rates in the lake.

The strong correlation between $Z_m$ and $R$ presumably occurs because higher sedimentation rates are accompanied by higher nutrient fluxes which support higher tubificid abundances which in turn produce deeper sediment mixing. If so, one would expect a correlation between $R$ and $Z_{90}$ to be positive but not as strong as between $Z_m$ and $R$ because of the biological variability inherent in the former comparison. This is indeed the case. Although biological processes are presumed to mediate the relationship between $R$ and $Z_m$, both variables are long-term averages which make no reference to biological effects. For the same reasons the correlations between $Z_m$ and flux of organic and inorganic carbon are high, with terriginous carbonates accounting for the positive correlation with $F_i$. The regression equations for $F_o$ versus $Z_m$, based on the present study and on a previous study in Lake Huron (Robbins 1982), illustrate (Fig. 4) the reproducibility of the relationship as well as the restricted range of mixed depths in Lake Huron. For a given mixed depth the organic carbon flux is roughly twice as high in Erie as in Huron.

Although we have shown that a highly significant correlation exists between the organic carbon flux and tubificid worm abundance in Lake Erie, the primary relationship is between the abundance of worms and the bulk sedimentation rate. Correlations between $N$ and $R$ and between $N$ and $F_o$ are statistically indistinguishable. Additional studies of sites localized within a single depositional basin (preferably the eastern basin), improved estimates of benthic abundance and seasonal variability plus a refined characterization of the nature of organic matter and its rate of degradation in surface sediments can be expected to further illuminate the role of nutrient supply rates in the regulation of tubificid abundances.

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# Role of Off-Channel Ponds in the Life Cycle of Coho Salmon (*Oncorhynchus kisutch*) and Other Juvenile Salmonids in the Coldwater River, British Columbia

S. Swales[1] and C. D. Levings

*West Vancouver Laboratory, Biological Sciences Branch, Department of Fisheries and Oceans, West Vancouver, B.C. V7V 1N6*

Swales, S., and C. D. Levings. 1989. Role of off-channel ponds in the life cycle of coho salmon (*Oncorhynchus kisutch*) and other juvenile salmonids in the Coldwater River, British Columbia. Can. J. Fish. Aquat. Sci. 46: 232–242.

Off-channel ponds in the upper reaches of the Coldwater River, British Columbia, were major rearing areas for juvenile coho salmon (*Oncorhynchus kisutch*). Chinook salmon (*Oncorhynchus tshawytscha*), steelhead trout (*Salmo gairdneri*), and Dolly Varden char (*Salvelinus malma*) were generally scarce in the ponds, although they were numerous in the main river. Coho salmon were predominant at "natural" river sites while steelhead trout was the main species at sites with "rip-rap" bank stabilization. Catches of juvenile coho were much lower in the main river than in the ponds where they were the main species, and were more variable in the river. Population density and biomass estimates of juvenile coho in the ponds ranged from 0.100 fish·$m^{-2}$ and 1.00 g·$m^{-2}$ to 1.00 fish·$m^{-2}$ and 5.15 g·$m^{-2}$, compared with density estimates of 0.08–0.23 fish·$m^{-2}$ in the river. The coho population in the ponds consisted of 0+ and 1+ age-groups in similar proportions, while in the main river the 0+ age-group was much more abundant. The growth rate of coho in the ponds was faster than in the main river, with pond fish reaching mean lengths of 62–79 mm at the end of the first growing season, compared with 53 mm in the main river. Smolt outmigration from the main study pond occurred in late spring with peak outmigration in May and June coinciding with peak river discharge and increasing water temperatures in the main river and pond.

Les cuvettes situées hors du chenal du cours supérieur de la rivière Cold Water, Colombie-Britannique, constituent des secteurs d'élevage de première importance pour les saumons coho juvéniles (*Oncorhynchus kisutch*). Dans ces cuvettes, on trouve généralement peu de saumon quinnat (*Oncorhynchus tshawytscha*), de truite arc-en-ciel (*Salmo gairdneri*) et de Dolly Varden (*Salvelinus malma*), bien qu'il y en ait beaucoup dans le cours principal de la rivière. Le coho est prédominant dans les endroits à l'état naturel tandis que la truite arc-en-ciel constitue l'espèce principale dans les endroits où les berges ont été stabilisées avec des enrochements. La capture de cohos juvéniles est nettement inférieure dans le cours principal à ce qu'elle est dans les cuvettes où cette espèce est prédominante; la capture est également plus variable dans la rivière que dans les cuvettes. Dans ces dernières, la densité de population des cohos juvéniles a été évaluée entre 0,100 poisson·$m^{-2}$ et 1,00 poisson·$m^{-2}$, et la biomasse a été évaluée entre 1,00 g·$m^{-2}$ et 5,15 g·$m^{-2}$, à comparer à une densité évaluée entre 0,08–0,23 poisson·$m^{-2}$ dans la rivière. La population de cohos dans les cuvettes est constituée de sujets appartenant aux groupes d'âge 0+ et 1+, en proportion semblable, alors que dans le cours principal, le groupe d'âge 0+ est beaucoup plus abondant. La vitesse de croissance du coho dans les cuvettes est supérieure à ce qu'elle dans le cours principal : dans les cuvettes, les sujets atteignent une longueur moyenne de 62–79 mm à la fin de la première saison de croissance, à comparer à 53 mm dans le cours principal. L'émigration des tacons s'est produite à la fin du printemps dans la cuvette d'étude principale, avec un maximum en mai et juin qui coïncidait avec le débit de pointe de la rivière et le réchauffement de l'eau dans le cours principal et dans la cuvette.

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In a recent study of the winter habitat preferences of juvenile salmonids in the Coldwater and Nicola rivers in south-western, interior British Columbia (Swales et al. 1986) small, off-channel ponds were found to be major overwintering areas for juvenile coho salmon (*Oncorhynchus kisutch*). Catches of coho salmon in the ponds were up to five times greater than in the best main river habitat, with an overwintering population of approximately 4000 juvenile coho in a 1 ha pond. In the upper reaches of the Coldwater (River), ponds appeared to provide more favourable overwintering habitat than main river areas, with coho in the ponds showing a greater mean length than main river fish and a high overwinter survival.

Ponds and other shallow, still-water, off-channel habitats have also been identified as major overwintering areas for juvenile coho in many coastal streams and rivers in British Columbia and the Pacific northwest. In the Clearwater R. in Washington, large numbers of juvenile coho overwintered in two small spring ponds close to the main river, migrating into the ponds from the main river in autumn (Peterson 1980, 1982a,

[1]Author to whom correspondence should be addressed. Present address: Department of Biological Science, University of Waikato, Hamilton, New Zealand.

1982b). After overwintering in the ponds, coho migrated out as smolts the following spring. In Carnation Creek, on the west coast of Vancouver Island, coho salmon use side-pools, which are dry during the summer but flooded in winter, as overwintering areas (Brown 1985; Bustard and Narver 1975; Hartman and Brown 1987; Tschaplinski and Hartman 1983). A recent study also showed that small, shallow lakes in the Keogh R. drainage in northern Vancouver Island are also significant overwintering areas for juvenile coho (Swales et al. 1988).

Juvenile coho in coastal streams and rivers generally migrate into ponds and other off-channel areas in fall and early winter, presumably to avoid high river flows typical of coastal areas with higher winter rainfall (Bustard and Narver 1975; Cederholm and Scarlett 1981; Peterson 1982b). Highest flows in many interior (noncoastal) rivers, however, often occur in early summer when increasing air temperatures melt snowpack in upland regions. There is evidence that juvenile salmonids in interior rivers move into ponds and other off-channel areas much earlier in the year than in coastal rivers to avoid freshet conditions in the main river (Bustard 1986). In addition to their role as refuge areas, off-channel ponds in interior rivers may therefore also form important summer rearing areas for juvenile salmonids (Bustard 1986).

The finding that large numbers of juvenile coho salmon overwintered in off-channel ponds in the Coldwater and Nicola Rivers provided a valuable opportunity to carry out more extensive investigations into the role of off-channel ponds in the life cycle of coho salmon and other juvenile salmonids in an interior river system. The preliminary winter study of 1984–85 was therefore continued through 1985 and early 1986 to provide information on the utilization of pond habitats during the annual life cycle of juvenile salmonids in the river.

## Study Area

The Coldwater R. is a tributary of the Nicola R. which discharges into the Thompson R. in the Fraser R. watershed. The river drains an area of 914 km$^2$ and is characterised by a moderate gradient with a broad, unstable floodplain. Winter is usually a period of minimum flows, low air temperatures, and heavy snowfall. Increasing temperatures in spring and early summer melt the snowpack, producing freshet conditions which continue until around the end of June. The mean discharge of the river at Merritt, where it joins the Nicola River, was 6.62 $m^3 \cdot s^{-1}$ in 1985, with a daily maximum and minimum of 67.5 and 0.23 $m^3 \cdot s^{-1}$ on May 19 and August 30, respectively (Water Survey of Canada 1986). A major new highway, linking the towns of Hope and Merritt, was under construction along the Coldwater R. valley during the period of the study.

All the study sites (Table 1) on the Coldwater R. were situated in the upper reaches of the river above Kingsvale (Fig. 1) at an altitude of about 1000 m above sea level. Much of the Coldwater R. valley in this region can be considered floodplain and there are extensive wetlands containing a number of permanent shallow ponds which drain into the river. Most of the ponds are either groundwater or spring fed and are inhabited by beavers (*Castor canadensis*). Three natural ponds in this area (C1, C2, and C3) were selected for study. All ponds were small in surface area (0.1–1 ha), shallow (mean depth 1–2 m), and surrounded by a mixed shoreline vegetation of willow (*Salix* sp.) and alder (*Alnus* sp.). The shallow margins of the ponds were characterised by emergent sedges (*Carex* sp.), while in pond C1 there was also a thriving growth of submerged aquatic vegetation. Pond C1 (surface area 1.0 ha) was the largest of the three ponds and was connected to an upstream pond of similar size. A high beaver dam on the outlet stream prevented fish from gaining access to the second pond. Ponds C2 and C3 were smaller (0.10 and 0.13 ha, respectively) than pond C1 and were situated approximately 10 km upstream (Fig. 1). The substrate in all ponds consisted of decaying organic matter overlaying mud and silt. A series of 12 small artificial ponds (each 0.1 ha in area) were constructed in August 1985 close to the Coldwater R. 5 km downstream from pond C1, as part of a habitat restoration programme. Limited investigations were carried out in fall 1985 on the fish populations in one pond (C4).

Four study sites were selected on the mainstream Coldwater R. above Kingsvale (Fig. 1). Sites A1 and A2, located in the upper reaches of the river, were characterized by pools and riffles with abundant bankside vegetation and instream organic debris. Sites B1 and B2 were situated 15–20 km downstream of sites A1 and A2. These sites showed less habitat diversity than the upstream sites, with one bank at each site consisting of "rip-rap" bank stabilization boulders (diameter 0.5–1.5 m) which replaced the natural bankside habitat. Instream organic debris was sparse and the channel consisted of a shallow glide (mean depth 1 m), with little evidence of a pool-riffle pattern.

Two ponds (N1, N2) situated close to the Nicola R. below Merritt (Fig. 1) were also investigated. Pond N1 was a small (0.5 ha), isolated cut-off pond, while pond N2, situated 30 km downstream, was larger (1.0 ha) and one of a series of three interconnected ponds in a wetland area close to the river.

The Coldwater and Nicola rivers support populations of coho salmon, chinook salmon (*O. tshawytscha*), steelhead trout (*Salmo gairdneri*), Dolly Varden char (*Salvelinus malma*), and mountain whitefish (*Prosopium williamsoni*). Annual salmon

TABLE 1. Summary of the dimensions and habitat characteristics of pond and river sites.

| | Ponds | | | | | | River | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Parameter | C1 | C2 | C3 | C4[a] | N1 | N2 | A1 | A2 | B1 | B2 |
| Mean width (m) | — | — | — | — | — | — | 3–5 | 4–8 | 5–10 | 5–10 |
| Sample length (m) | — | — | — | — | — | — | 25 | 16 | 26 | 26 |
| Mean depth (m) | 1–2 | 1 | 1–2 | 2 | 2 | 1–2 | 0.5–1.0 | 0.5–1.0 | 0.5–1.5 | 0.5–1.0 |
| Area (ha) | 1.00 | 0.10 | 0.13 | 0.01 | 1.20 | 1.00 | 0.01 | 0.01 | 0.02 | 0.02 |
| Substrate | Decaying organic matter/mud, silt | | | | | | Gravel/cobbles | | | |
| Bankside characteristics | Emergent grasses and sedges, trees, and shrubs | | | | | | Trees, shrubs | | Rip-rap boulders/ cobbles | |

[a]Recently constructed pond; no bankside vegetation.

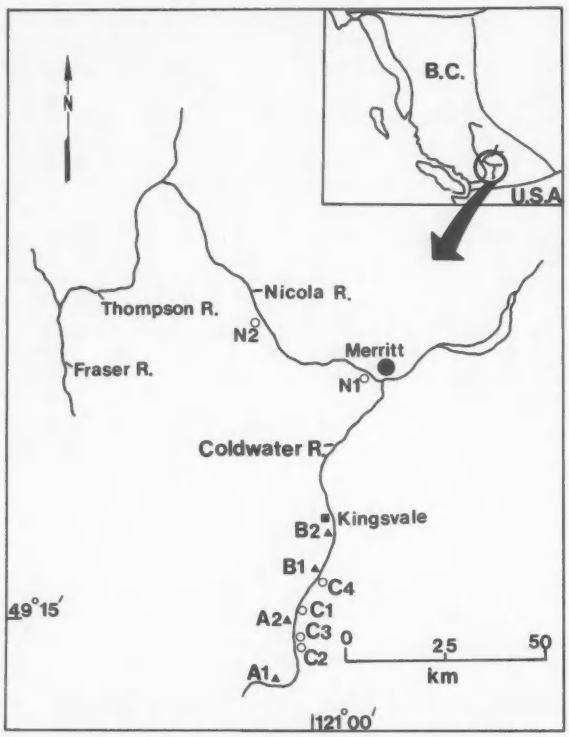


FIG. 1. Location of study area and main river (▲) and pond (○) sampling sites in the Coldwater and Nicola rivers. The following site key can be used to find the exact locations, described in detail in Lauzier and McPherson (1986): Al = 7; A2 = 4, B1 = 6; B2 = 7; C1 = 5.2; C4 = 6p; N1 = 18c; N2 = 28P.

escapement estimates are highly variable. Over the period 1968–78 coho escapements in the Coldwater R. ranged between 70–1500 and averaged 600 and 935 for coho and chinook salmon, respectively (Brown et al. 1979). Wild stocks are also supplemented by the introduction of hatchery-reared juveniles, with approximately 60 000 hatchery-reared coho salmon (mean weight 5 g) being stocked into the Coldwater River in April 1985. Juvenile steelhead trout are also stocked annually in large numbers.

## Materials and Methods

### General Fish Sampling

Routine fish sampling in ponds and main river sites was carried out over the period January – November 1985. Soft substrate conditions and extensive marginal vegetation in all ponds rendered conventional sampling techniques such as netting ineffective. Similarly, deep (1m+) pools at some main river sites precluded efficient sampling by electrofishing. "Gee"[2] wire-mesh traps were used and found to be an effective sampling method in both ponds and main river sites for obtaining representative samples of coho salmon and Dolly Varden char within the size-range 50–130 mm (Swales 1987). Trap catches can provide estimates of relative abundance through catch-per-unit-effort (CPUE). We assume equal catchability of traps in all habitats. However, it is possible that traps are not equally effective in all habitats since differences in habitat characteristics between sites may affect fish catchability (Bloom 1976; Swales 1987). However, we felt that the advantage of using the same sampling method in all sites outweighed possible disadvantages due to differences in trap catchability.

Traps were baited with approximately 2 g of salmon roe and set on the substrate at each site, attached to the bank by an anchoring rope. The standard soak-time (the interval between setting and retrieval) at each site was 24 h. CPUE was defined as the catch (number of individuals of particular species in a trap) within this time period. Mean CPUE was calculated using separate trap data for the period under consideration. The number of traps set at main river sites ranged from 8–15, while up to 30 traps were set at pond sites on each sampling occasion. Traps were generally set around pond margins at 5 m intervals, within 1–2 m of shore. The distribution of fish in pond C1 was also investigated by setting traps on transects close to the bank and in offshore areas. Traps in main river sites were set in a representative selection of microhabitats within the study area.

Population estimates at main river sites were made in August 1985, during a low flow period, using a combination of electrofishing and netting. The presence of deep, fast-flowing runs and pools at some sites meant that the efficiency of electrofishing was often relatively low. A minimum population estimate was therefore made by using a combination of electrofishing and netting. Electrofishing was carried out using a Smith Root backpack-style electrofisher (Model 11A), while netting was undertaken using a 25-m seine net (mesh size 1 cm). A short section of river (16–25 m; Table 1) was isolated using stop nets installed across the channel. Three successive electrofishing runs were then made in an upstream direction. The fish captured in each run were kept in a holding container until the end of sampling operations. Following the completion of electrofishing operations, three successive sweeps with the seine net were made through the section between the stop nets. Generally, few fish were captured by the end of the last netting, suggesting that a high proportion of the population had been sampled. The total number of fish captured by electrofishing and netting was taken as the minimum population estimate. All fish captured were identified, enumerated, measured in length to the nearest 1 mm and a scale sample taken for later age determination.

All mainstem Coldwater R. sites and pond C1 were sampled by trapping at approximately monthly intervals during the study period. Ponds C2 and C3 were sampled monthly over the period June–November 1985, while ponds C4, N1, and N2 were sampled less regularly at various times during the fall–winter.

Population estimates of juvenile salmonids in ponds C1, C2, and C3 and main river sites were made at intervals during the study period. The size of the juvenile salmonid population in pond sites was determined by mark–recapture. Fish were captured by trapping over a 5-d period and all fish marked by freeze branding and fin clipping and then returned alive to the pond. Traps were reset in the pond 2 wk later and the numbers of marked and unmarked fish recorded. Population estimates were made using the modified Peterson estimate (Ricker 1975). A subsample of fish was measured in length to the nearest millimetre and weighed to the nearest 0.1 g using an electronic balance.

[2]Cuba Speciality Manufacturing Co., Ridgeway, Ontario.

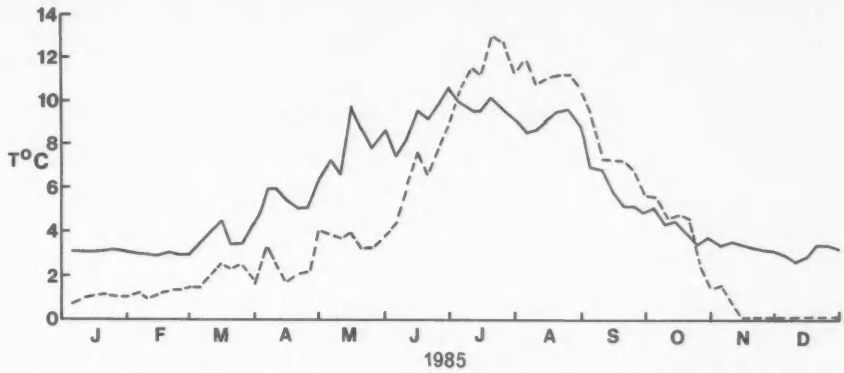


FIG. 2. Water temperatures in the mainstem Coldwater R. (broken line) and pond C1 (solid line) during 1985.

TABLE 2. Trap catches of juvenile salmonids captured at each site over the study period. *C* = total catch, % = proportion of the total catch, CPUE = mean catch of each species calculated using separate trap data.

| | | Coho salmon | | | Chinook salmon | | | Steelhead trout | | | Dolly Varden char | | | All species | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | Traps set | *C* | % | CPUE | *C* | % | CPUE | *C* | % | CPUE | *C* | % | CPUE | *C* | CPUE |
| River | | | | | | | | | | | | | | | |
| A1 | 92 | 143 | 61 | 1.70 | 18 | 8 | 0.01 | 45 | 19 | 0.08 | 29 | 12 | 0.23 | 235 | 2.00 |
| A2 | 97 | 172 | 64 | 2.83 | 45 | 17 | 0.31 | 31 | 12 | 0.18 | 20 | 7 | 0.20 | 268 | 3.30 |
| B1 | 71 | 68 | 26 | 0.63 | 62 | 24 | 0.36 | 127 | 48 | 1.16 | 5 | 2 | 0.07 | 262 | 2.10 |
| B2 | 78 | 84 | 34 | 0.84 | 45 | 18 | 0.34 | 117 | 48 | 1.20 | 0 | 0 | 0 | 246 | 2.40 |
| Ponds | | | | | | | | | | | | | | | |
| C1 | 383 | 1207 | 96 | 5.00 | 21 | 2 | 0.10 | 30 | 2 | 0.07 | 3 | 0.2 | 0.01 | 1261 | 5.20 |
| C2 | 117 | 322 | 88 | 2.50 | 32 | 9 | 0.14 | 5 | 1 | 0.05 | 5 | 1 | 0.04 | 364 | 2.75 |
| C3 | 115 | 644 | 95 | 10.60 | 32 | 5 | 0.34 | 2 | 0.3 | 0.05 | 3 | 0.3 | 0 | 681 | 11.10 |
| C4 | 25 | 144 | 75 | 12.80 | 2 | 1 | 0.40 | 45 | 24 | 3.80 | 0 | 0 | 0 | 191 | 17.00 |
| N1 | 55 | 132 | 92 | 3.10 | 12 | 8 | 0.30 | 0 | 0 | 0 | 0 | 0 | 0 | 144 | 3.40 |
| N2 | 35 | 33 | 15 | 1.40 | 173 | 80 | 6.00 | 9 | 4 | 0.30 | 0 | 0 | 0 | 215 | 7.70 |

### Smolt Outmigration Census

Coho salmon smolts and other juvenile salmonids emigrating from pond C1 over the period April 9 – June 15, 1986 were trapped using a fence trap (Conlin & Tutty 1979) installed in an outlet stream below a small beaver dam. The fence was made of 5-mm plastic "Vexar" screening material and was constructed across the channel immediately below the dam. A 3-m aluminium pipe (diameter 20 cm) was positioned horizontally in the outlet stream, with one end inserted through the fence and the other end leading into a live box (dimensions 1.5 m × 1 m × 1 m) positioned in the outlet stream. It was unlikely that large numbers of fish left the pond via another outlet present on the pond, due to the impermeable nature of this particular dam. However, the possibility that fish did leave the pond via this route cannot be discounted. The trap was checked daily whenever possible and all trapped fish identified, enumerated, measured in length to the nearest millimetre and a subsample weighed to the nearest 0.1 g. All fish were released alive into the Coldwater R. below the trap.

### Physical Measurements

Water temperature in pond C1 and the nearby mainstem Coldwater R. was monitored continuously over the study period using "Weksler" 30-d thermographs, with probes set at a depth of 1 m. Chart temperature readings were checked monthly using a pocket thermometer. The error was generally less than 1°C and never more than 2°C. Daily averages, calculated from chart readings made at 0600, 1200, 1800, and 2400 h, were used to determine 5-d means.

## Results

### Water Temperature

Water temperature measurements in pond C1 and the nearby mainstem Coldwater R. during 1985 (Fig. 2) show that the pond (mean = 5.5°C (SD 2.5°C)) was consistently warmer than the river (mean = 2.9°C (SD 2.2°C)) from January until the end of June. The temperature difference between the two sites over this period ranged from 1 to 5.5°C. The temperature pattern was reversed from the beginning of July to the middle of October, with the river (mean = 9.3°C (SD 2.8°C)) being consistently warmer than the pond (mean = 7.7°C (SD 2.1°C)). The temperature was again reversed from the middle of October to the end of the year with the pond being warmer than the river by 2–3°C.

### Species Composition

Five species of juvenile salmonid (coho salmon, chinook salmon, steelhead trout, mountain whitefish, and Dolly Varden

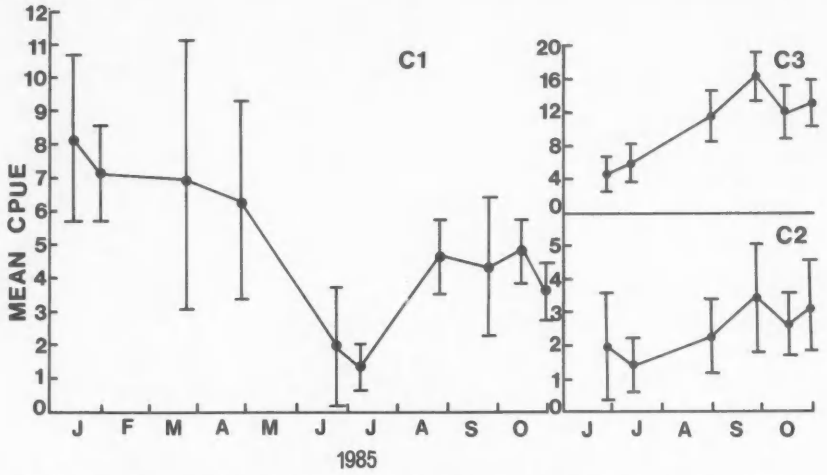


FIG. 3. Mean catch-per-unit-effort (CPUE) (with 95% C.L.) of juvenile coho salmon in ponds C1, C2, and C3 during 1985.

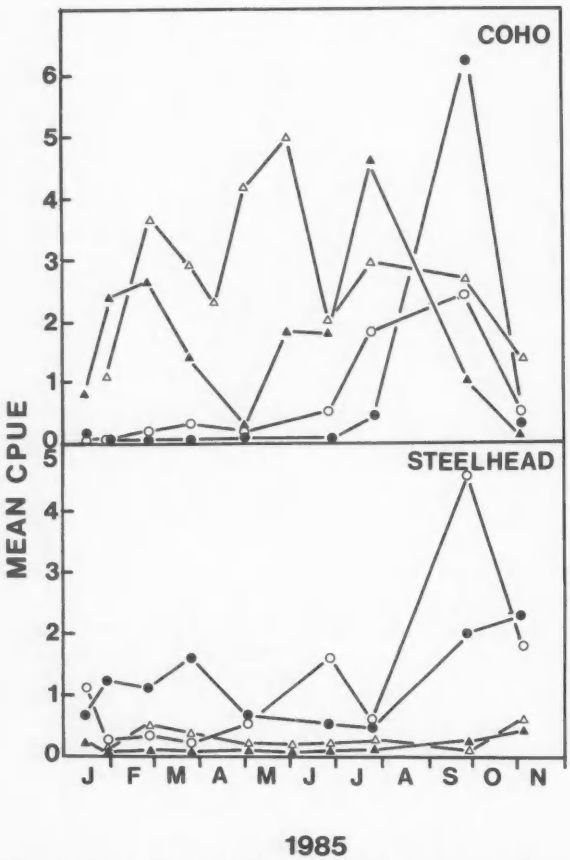


FIG. 4. Mean catch-per-unit-effort (CPUE) of juvenile coho salmon and steelhead trout in mainstem Coldwater R. sites during 1985. Key to sites; A1 (▲), A2 (Δ), B1 (●), B2 (○).

char) were captured during the study. Coho salmon formed the largest proportion of the total catch at most pond sites (Table 2). Juvenile coho formed from 75 to 96% of the total catch in ponds C1 – C4, and N1 with chinook salmon, steelhead trout, and Dolly Varden char comprising the remainder of the catch. Chinook salmon was the predominant juvenile salmonid in pond N2, forming 80% of the total catch, with coho salmon being much less numerous than in the other ponds. Steelhead trout and Dolly Varden char generally formed a small proportion of the total pond catches. In the newly constructed artificial pond, C4, steelhead trout fry were relatively abundant, forming 24% of the total catch.

Coho salmon was the predominant juvenile salmonid at sites A1 and A2 in the mainstem Coldwater R., where they formed around 60% of the total catch (Table 2). Chinook salmon, steelhead trout, and Dolly Varden char generally formed a much smaller proportion of the catch at these sites, with each species ranging from 7 to 19% of the total catch. Coho salmon were less numerous at sites B1 and B2, forming around 30% of the total catch, while steelhead trout were more evident, comprising almost half the total catch. Chinook salmon were more abundant here than at sites A1 and A2, forming 18–24% of the total catch.

## Trap Catches

Trap catches of juvenile salmonids over approximately 50 mm in length at most mainstem Coldwater R. sites were generally low (Table 2). Mean CPUE for individual species at sites A1 and A2 ranged from 1.7–2.8 for coho salmon to less than 0.3 for chinook salmon, steelhead trout, and Dolly Varden char. Similarly, mean CPUE at sites B1 and B2 ranged from a high of 1.2 for steelhead trout to 0.6–0.8 for coho salmon and 0.3 for chinook salmon.

In contrast, catches at most pond sites were generally much higher (Table 2). Mean CPUE of coho salmon ranged from a minimum of 1.4 in pond N2 to a maximum of 12.8 in pond C4. Catches of other salmonids were generally much lower, usually less than 1.0, except at ponds N2 and C4 where chinook salmon and steelhead trout were abundant, respectively.

TABLE 3. Population estimates of coho and chinook salmon in ponds C1, C2, and C3 at intervals during the study period. N = population size, $B$ = population biomass, $W$ = mean weight (g), 95% C.L. = 95% confidence limits, SD = standard deviation.

| Site | Date | Species | Age-group | $N$ | 95% C.L. | $N$ ($m^{-2}$) | $W$ | (SD) | $B$ (kg) | $B$ ($gm^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| Pond C1 | 01.31.85 | coho | 0+ | 1500 | (1152–2038) | 0.150 | — | | — | — |
| | | | 1+ | 2249 | (1658–2933) | 0.225 | — | | — | — |
| | | chinook | 0+ | 75 | (43–92) | 0.008 | — | | — | — |
| | 11.01.85 | coho | 0+ | 437 | (308–651) | 0.044 | 4.5 | (1.3) | 2.000 | 0.20 |
| | | | 1+ | 655 | (443–938) | 0.066 | 12.8 | (3.7) | 8.384 | 0.84 |
| | 04.21.86 | coho | 0+ | 408 | (285–720) | 0.041 | 6.1 | (1.7) | 2.500 | 0.25 |
| | | | 1+ | 613 | (411–1037) | 0.061 | 12.8 | (2.5) | 7.850 | 0.79 |
| Pond C2 | 11.01.85 | coho | 0+ | 63 | (47–88) | 0.063 | 5.7 | (1.1) | 0.360 | 0.36 |
| | | | 1+ | 180 | (135–252) | 0.180 | 11.6 | (1.3) | 2.088 | 2.10 |
| | | chinook | 0+ | 34 | (18–109) | 0.034 | 5.7 | (0.6) | 0.194 | 0.19 |
| | 04.21.86 | coho | 0+ | 26 | (17–45) | 0.026 | 7.0 | (0.8) | 0.182 | 0.18 |
| | | | 1+ | 73 | (49–129) | 0.073 | 11.4 | (1.5) | 0.832 | 0.83 |
| | | chinook | 0+ | 53 | (26–264) | 0.053 | 6.0 | (0.8) | 0.318 | 0.32 |
| Pond C3 | 11.01.85 | coho | 0+ | 483 | (410–578) | 0.372 | 3.0 | (0.9) | 1.449 | 1.15 |
| | | | 1+ | 822 | (697–984) | 0.632 | 6.3 | (1.0) | 5.179 | 4.00 |
| | | chinook | 0+ | 329 | (169–1233) | 0.253 | — | — | — | — |
| | 04.21.86 | coho | 0+ | 270 | (229–324) | 0.208 | 3.6 | (1.1) | 0.972 | 0.75 |
| | | | 1+ | 460 | (391–552) | 0.354 | 7.5 | (1.3) | 3.450 | 3.45 |
| | | chinook | 0+ | 103 | (60–256) | 0.079 | 2.5 | (0.7) | 0.258 | 0.20 |

TABLE 4. Population estimates of coho and chinook salmon, steelhead trout, and Dolly Varden char in pond outlet stream and mainstem Coldwater River sites.

| Site | Date | Species | Age | $N$ ($m^{-2}$) |
|---|---|---|---|---|
| Pond C1 outlet stream No. 2 | 05.02.85 | coho | 0+ | 0.207 |
| | | | 1+ | 0.036 |
| | | chinook | 0+ | 0.007 |
| | | steelhead | 0+ | 0.108 |
| | | | 1+ | 0.045 |
| A1 | 08.21.85 | coho | 0+ | 0.008 |
| | | steelhead | 0+ | 0.075 |
| | | Dolly Varden | 0+ | 0.017 |
| | | | 1+ | 0.013 |
| | | | 2+ | 0.013 |
| A2 | 08.21.85 | coho | 0+ | 0.193 |
| | | | 1+ | 0.040 |
| | | chinook | 0+ | 0.133 |
| | | | 1+ | 0.007 |
| | | steelhead | 0+ | 0.087 |
| | | | 1+ | 0.027 |
| | | | 2+ | 0.013 |
| | | Dolly Varden | 2+ | 0.021 |
| B1 | 08.30.85 | coho | 0+ | 0.005 |
| | | | 1+ | 0.004 |
| | | chinook | 0+ | 0.042 |
| | | steelhead | 0+ | 0.062 |
| B2 | 08.30.85 | coho | 0+ | 0.051 |
| | | chinook | 0+ | 0.100 |
| | | steelhead | 0+ | 0.340 |
| | | | 1+ | 0.022 |
| | | | 2+ | 0.006 |

Mean CPUE of juvenile coho in ponds C1, C2, and C3 varied considerably over the year (Fig. 3). Catches in pond C1 were highest at the beginning of the year, but by June and July had declined considerably. Although catches increased later, catches did not reach the levels recorded at the beginning of the year. A similar upward trend in catches from June to the end of the year was also seen in catches of coho in ponds C2 and C3 (Fig. 3). Catches were consistently much higher in pond C3 than in the other ponds.

Catches of coho salmon and steelhead trout in the mainstem Coldwater R. showed more marked variation between sites and sampling occasions than at pond sites (Fig. 4). Catches of coho salmon were consistently higher over the years at sites A1 and A2, than at B1 and B2, where steelhead trout were predominant. Catches of both species declined in spring (March to April), coinciding with the outmigration of large numbers of smolts from the river. There was a marked increase in catches of both species at sites B1 and B2 in September, which was not evident at sites A1 and A2, where catches declined. The increase in coho catches at A1 and A2 in early summer was largely attributable to the introduction of large numbers of hatchery-reared coho into the river at this time, while the increased catches at sites B1 and B2 in autumn may have been an indication of a prewinter outmigration from the river. No hatchery-reared coho, as indicated by adipose fin clips and size differences, were captured in any of the off-channel ponds. Catches of wild juvenile coho were significantly higher in ponds C1, C2, and C3 than in the mainstem Coldwater R. (Table 2). (Students $t = -5.19$, $P < 0.005$, d.f. = 56). There was a significant difference in the catches of juvenile coho between ponds C1, C2, and C3 (Kruskal–Wallis ANOVA; $H = 10.6$, $P < 0.001$) with catches being much higher in C3. Mann–Whitney "$U$" tests revealed significant differences between sites A1 and A2 and sites B1 and B2 in the catches of coho salmon ($U = 70$; $P < 0.002$) and steelhead trout ($U = 38$; $P < 0.002$). Coho catches were higher at A1 and A2, compared with B1 and B2. Steelhead catches were higher at B1 and B2.

The distribution pattern of juvenile coho in pond C1 was investigated on May 2 and July 9, 10, 1985, when traps were set around the margins of the pond, within 1 m of shore, and along a transect along the centre of the pond, equidistant from each shore. Catches on both occasions were higher along the shore than in the offshore traps, with mean CPUE ranging from 1.1 to 8.7 in bankside traps (mean 3.7) and 0.2–2.7 in offshore traps (mean 1.3).

## Population Estimates

Population estimates of juvenile salmonids in ponds C1, C2, and C3 made during the study period are shown in Table 3.

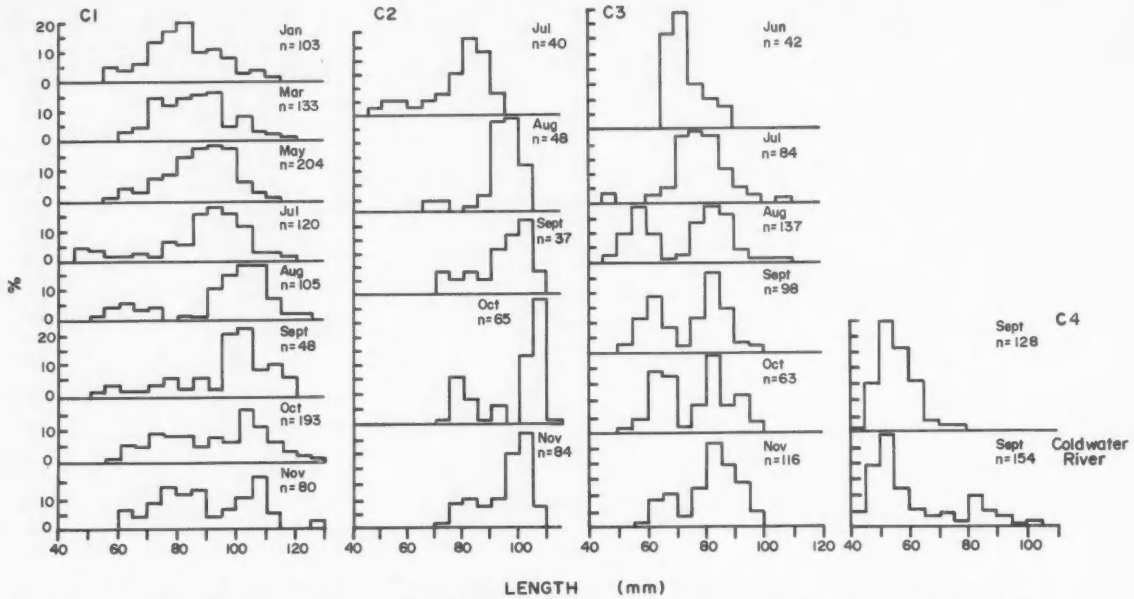


FIG. 5. Length-frequency histograms of wild juvenile coho salmon in ponds C1–C4 and the mainstem Coldwater R. during 1985.

TABLE 5. Relative proportions and mean lengths of the 1984 and 1985 cohorts of juvenile coho salmon captured in ponds C1, C2, C3, C4, and the mainstem Coldwater River during fall 1985. $N$ = sample size, % = proportion of the total catch, $L$ = mean length (mm) ±95% C.L.

| Site | Cohort | $N$ | % | $L$ ± 95% C.L. |
|---|---|---|---|---|
| C1 | 1985 | 182 | 41 | 72.2 ± 1.2 |
| | 1984 | 261 | 59 | 103.4 ± 1.4 |
| C2 | 1985 | 38 | 26 | 78.5 ± 1.9 |
| | 1984 | 110 | 74 | 99.2 ± 1.2 |
| C3 | 1985 | 66 | 37 | 62.4 ± 1.4 |
| | 1984 | 111 | 63 | 84.2 ± 1.9 |
| C4 | 1985 | 128 | 100 | 55.0 ± 1.2 |
| Mainstem Coldwater River | 1985 | 123 | 78 | 52.7 ± 1.3 |
| | 1984 | 34 | 22 | 82.3 ± 1.7 |

Coho salmon were most abundant in all ponds, with lesser numbers of chinook salmon (steelhead trout and Dolly Varden char were captured in only small numbers and population estimates could not be made due to low recapture rates). The population density and biomass of coho salmon (combined age-groups) ranged from minima of 0.100 fish·m$^{-2}$ and 1.00 g·m$^{-2}$ in pond C2 to maxima of 1.00 fish·m$^{-2}$ and 5.15 g·m$^{-2}$ in pond C3 in November 1985. The largest coho population recorded was in pond C1 in January 1985, when approximately 4000 coho were overwintering in the pond. The coho population in the pond had declined by fall 1985 to approximately 1000 fish. Overwinter survival from fall 1985 to spring 1986 ranged from an estimated 93% in pond C1 to 41% in pond C2 and 56% in pond C3.

The population density of coho salmon in August at mainstem Coldwater R. sites was generally lower than in the ponds (Table 4), ranging from 0.008 fish·m$^{-2}$ in site A1 to 0.233 fish·m$^{-2}$ in site A2. Moderately high densities of coho salmon were recorded in outlet stream No. 2 of pond C1 in May 1985. Steelhead trout and chinook salmon were also recorded at moderate densities at sites A2 and B2. Dolly Varden char were present at low densities only at sites A1 and A2.

## Population Structure

Monthly length-frequency histograms of juvenile coho salmon trapped in ponds C1–C4 and the mainstem Coldwater R. during 1985 are shown in Fig. 5. The 1984 and 1985 cohorts were predominant in ponds (Table 5), with small numbers remaining from the 1983 cohort also being taken in pond C1 prior to smolt outmigration in June. It is likely that the population size of the 1985 cohort in the ponds in early summer was underestimated from trap catches since fry less than about 50 mm in length were able to escape through the trap mesh. The growth in length of each cohort over the year in pond C1 is clearly evident in Fig. 5. Population size and age structure varied considerably between sites. The 1984 cohort of coho salmon was predominant in catches in ponds C1, C2, and C3 during fall, ranging from 59 to 74% of the total catch, while the 1985 cohort was predominant in the mainstem Coldwater R. and pond C4 (Table 5).

## Size Variation

The mean length of the 1985 cohort of coho salmon in fall 1985 ranged from a minimum of 52.7 mm in the mainstem Coldwater R. to a maximum of 78.5 mm in pond C2 (Table 5). The 1984 cohort ranged from a maximum of 103.4 mm in pond C1 to a minimum of 82.3 mm in the mainstem Coldwater R. There were significant differences using parametric ANOVA between ponds C1, C2, and C3 in the mean lengths of both 1985 ($F = 54.7$, $P < 0.01$, d.f. = 148) and 1984 ($F = 65.4$, $P < 0.001$, d.f. = 146) cohorts of juvenile coho. The mean lengths of both cohorts were considerably greater in ponds C1 and C2 than in pond C3, where coho were only slightly, but significantly ($P < 0.05$), larger than in the mainstem Coldwater R. Coho captured in pond C1 during 1985 were consistently

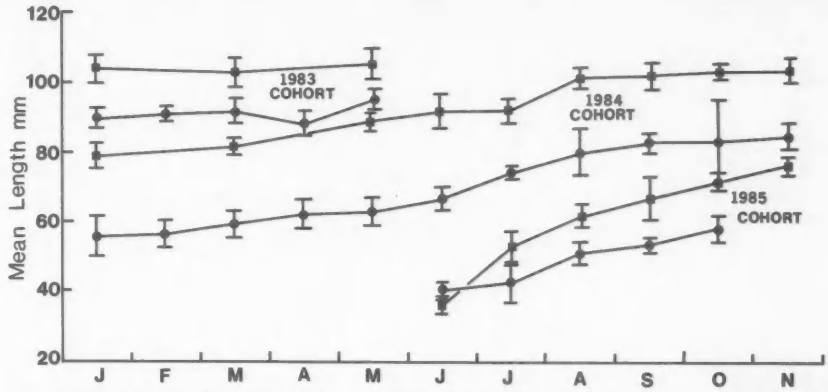


FIG. 6. Mean lengths of the 1983, 1984, and 1985 cohorts of juvenile coho salmon in pond C1 (■) and the mainstem Coldwater R. (●) during 1985. Vertical lines indicate 95% C.L.

larger over the year than coho captured in the mainstem Coldwater R. (Fig. 6). Coho fry in pond C1 showed a much faster growth rate than mainstem coho, reaching a mean length of 76.0 mm by the end of the year, compared with 52.7 mm in mainstem fish. The size difference in the 1984 cohort was in the range 20–30 mm. The size advantage of pond coho over mainstem coho was maintained in all cohorts throughout the year.

### Smolt Outmigration

A total of 1257 coho salmon smolts, 62 steelhead trout, and 3 Dolly Varden char were trapped as they migrated out of pond C1 over the period April 10 – June 23, 1986. Coho smolts began to migrate out of the pond in mid-April, but it was not until early May that substantial numbers began to be recorded (Fig. 7). Catches increased during May and were highest in late May and early June, coinciding with freshet conditions in the river due to snowmelt and increased water temperatures in both pond and main river. Daily outmigration peaked at 152 coho smolts on May 22, approximately 5 d before the peak in river discharge (Fig. 7). Average daily catch increased from a mean of 4.5 ± 2.0 (± 95% C.L. (confidence limits)) in April to 33.5 ± 11.0 in May and 20.7 ± 6.3 in June. The mean length of coho smolts increased over the period of outmigration (Fig. 7). The increase was most pronounced during the first 5 wk of the outmigration, when weekly mean length increased from 86.8 ± 4.3 mm (±95%C.L.) in week 1 to 116.5 ± 2.5 mm in week 5. The mean length of steelhead trout trapped over the outmigration period was 128.6 ± 11.9 mm (±95%C.L.), with a size range of 60–267 mm.

## Discussion

### Movement of Coho Into Ponds

Off-channel ponds on the floodplain of the Coldwater R. play a major role in the life history of juvenile coho salmon in the river. The ponds are not only major overwintering habitats for coho (Swales et al. 1986) but are also important refuge and rearing areas during other seasons of the year. Variations in trap catches and population structure over the year suggest that most coho migrate into the ponds during early summer, when the main river is in freshet due to snowmelt. In this way, ponds and other off-channel areas appear to be seeded with coho fry, which hatch out in May and June, and older fish. When flows in the main river diminish later in the summer, a significant proportion of the coho remain in the ponds, where they continue to rear during the remainder of the year, migrating out as smolts in spring after overwintering in the ponds.

In coastal streams and rivers, most recruitment to off-channel habitats occurs typically in fall and winter in response to high water discharge in the main river. Only a few coho moved to these habitats in spring and summer at Carnation Creek, British Columbia (Bustard and Narver 1975) and the Clearwater River, Washington (Cederholm and Scarlett 1981). In a study of the role of riverine ponds in the production of coho salmon in the Clearwater River in Washington, Peterson (1980) found that most coho migrated into the pond as fingerlings in fall, with only limited immigration of fry in spring and summer. It was suggested that predation by large cutthroat trout (*Salmo clarki clarki*) in the ponds was a major factor limiting summer fry recruitment.

Major differences in flow regimes exist between coastal and interior rivers in British Columbia. The summer immigration of juvenile coho to off-channel ponds recorded in the Coldwater River may be indicative of a more general pattern of off-channel habitat utilization in interior rivers. Studies in the Morice River in northern British Columbia also showed that fry and yearling coho salmon migrated in large numbers into a small (0.5 ha) off-channel pond in early summer when the main river was in freshet (Bustard 1986). The pond provided coho with both a refuge from the high flow conditions in the main river and a productive summer rearing habitat. After overwintering in the pond, coho emigrated as smolts the following spring. The results of our study show that off-channel ponds play a similar role in the life cycle of coho salmon in the Coldwater River. Summer immigration of juvenile coho to off-channel ponds could be a strategy to avoid the high variable main-channel flows. Rearing and overwintering in the ponds is likely to be an adaptive strategy to exploit the more stable environmental conditions and food production. The faster growth of coho in off-channel ponds, compared with the main river, suggests that coho of a given age may smoltify earlier in the ponds than in the river.

### Pond Habitat and Coho Smolt Production

The variation in the abundance, structure, and growth rate of coho stocks between ponds may be attributable to several fac-

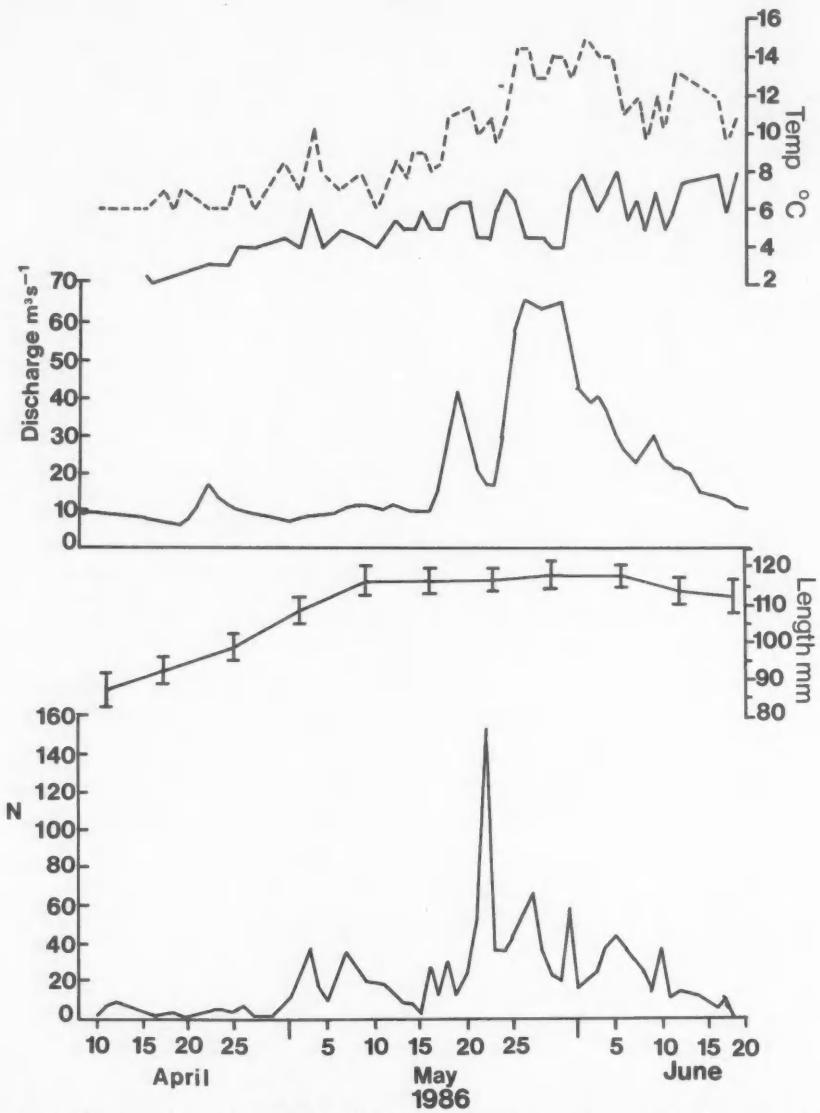


FIG. 7. Numbers and mean lengths (with 95% C.L.) of coho salmon smolts emigrating from pond C1, April – June 1985, together with river discharge measurements and water temperatures in pond C1 (broken line) and mainstem Coldwater R. (solid line).

tors. The ponds varied considerably in size, morphometry, accessibility to the main river, and predator populations. The size of the coho population in the ponds may depend on the size of the adult spawning population in the river and subsequent juvenile recruitment, as well as distance from the spawning grounds. Pond morphometry is also likely to play a major role in determining overwinter survival (Swales et al. 1986). The fact that the number of coho in pond C1 at the end of 1985 was only around 25% of the number at the start of the year suggests that fewer fish immigrated into the pond during 1985 than in the previous year. Though maximum daily discharge was slightly higher in 1985 than 1984 (Water Survey of Canada 1985), peak discharge was recorded earlier in the former year, and was of much shorter duration. These findings suggest that the size of pond coho populations may fluctuate considerably from year to year. The magnitude, timing, and duration of the peak summer flows in the main river may be major factors since in years of sustained high flows the river overflows onto its floodplain, merging with the off-channel ponds for considerable time periods. In these years, coho juveniles may find access to the ponds much easier than in years of lower flows or reduced duration of freshet.

The faster growth rate of coho in pond C1 than in main-channel fish may be attributable in part to the higher water temperatures in the pond during much of the year. Invertebrates in the pond were also abundant (Swales and Levings unpubl.

data), providing coho with a good food source. Differences in coho growth rates between ponds may be attributable to differences in pond morphometry, leading to variations in food availability and water temperature or to population density, with growth rate decreasing at higher densities due to increased intraspecific competition for food. Peterson (1980, 1982b) also found considerable growth differences between juvenile coho overwintering in Clearwater R. ponds and suggested that differences in pond morphometry may have affected food availability in the ponds. It is likely that water temperature, population density, and pond morphometry were all important contributory factors in explaining growth differences in juvenile coho in the Coldwater R. ponds.

Juvenile coho were closely associated with the shoreline areas of ponds. A recent study of juvenile coho overwintering in small lakes (8 and 25 ha) in northern Vancouver Island (Swales et al. 1988) also found that most juvenile coho were captured within a few metres of shore. In south-eastern Alaska, juvenile coho were most abundant close to shore in main-channel beaver ponds (Bryant 1984), and catches of juvenile coho in Great Central Lake, Vancouver Island, were also greatest in shoreline areas (Mason 1974). Juvenile coho also associate closely with bankside areas in streams and rivers, where they congregate near bankside roots, logs, undercut banks, and overhanging vegetation (Bustard and Narver 1975; Hartman 1965; Tschaplinski and Hartman 1983). The emergent vegetation in the shallow margins of pond C1 provided juvenile coho with both cover from predators and an abundant source of food. Shallow ponds have a high shoreline perimeter to surface area ratio as well as extensive bankside habitats, and these factors may be important in explaining the high densities of juvenile coho overwintering and rearing in the Coldwater R. ponds. As pointed out in our work on Vancouver Island lakes (Swales et al. 1988), shoreline perimeter may the most effective unit for coho production.

Smolt outmigration from pond C1 occurred over a similar time period to that recorded in the Morice River in northern British Columbia (Bustard 1986), although peak outmigration preceded that on the Morice River by around 3 wk. In both rivers, outmigration coincided with high main-channel discharges produced through snowmelt. Coho smolt outmigration in the Clearwater River ponds occurred between March and May but also coincided with high flows in the main river due to heavy rainfall (Peterson 1980).

The total coho smolt production from the Coldwater R. has been estimated from preliminary sampling to be around 30 000 or 300 smolts per kilometre of river (Wightman 1979). Our studies were unable to provide details on the production of coho in the main stem river compared with the ponds, and this clearly should be the next step to determine limiting factors for interior coho populations. However, we estimate that around 2000–3000 coho were produced from the three study ponds in 1985. This total represents approximately 5–10% of the estimated total production for the river, equivalent to the smolt yield from around 7–10 km of river. However, this may underestimate the total smolt production from off-channel ponds on the river as an unknown number of other ponds and off-channel habitats are present on the Coldwater River floodplain which may also be important coho production areas. Peterson (1980) estimated the coho smolt production from two riverine ponds on the Clearwater River to equal the smolt yield from 14 km of fully utilized Clearwater River tributary. In Carnation Creek, Vancouver Island, approximately 23% of coho smolt production is derived from off-channel areas (Brown 1985).

## Species Composition of Ponds

In Pacific Northwest river systems with off-channel ponds, juvenile coho salmon are usually the predominant juvenile salmonids in the ponds, as seen in the Coldwater River. Coho salmon were the dominant species in the Clearwater River ponds, although cutthroat trout were also present (Cederholm and Scarlett 1981). Over 96% of salmonid numbers and biomass in a small beaver pond close to Fish Creek in Oregon were composed of juvenile coho (Everest and Sedell 1983). Coho salmon also accounted for 60–90% of the catch in main-channel beaver ponds in south-eastern Alaska streams (Bryant 1984). In the summer rearing period, juvenile coho in the main river channel generally prefer pool areas with abundant cover (McMahon 1983). These habitat preferences of juvenile coho are probably major factors leading to the predominance of this species in off-channel ponds.

It may also be argued that the abundance of coho salmon in the Coldwater River ponds merely reflected the composition of the main river community. Most chinook spawn downstream of the ponds we studied. However, the size of the steelhead trout spawning populations in the river are often similar to or greater than the number of coho salmon (Brown et al. 1979), and this species was scarce in most ponds. The predominance of coho salmon in the ponds appears to be due predominantly to habitat preference factors, although other functional and biological factors cannot be ruled out (Swales et al. 1986). Unlike ponds studied elsewhere, predators such as larger Dolly Varden char and cutthroat trout were virtually absent from the Coldwater ponds. The predominance of juvenile chinook salmon in pond N2 appears to reflect the abundance of chinook salmon in the Nicola River and the low numbers of coho salmon, which apparently rear mainly in the Coldwater River and other tributaries. Chinook salmon are thought to use primarily cobble substrate and other cover as overwintering habitat (e.g. Hillman et al. 1987), and are present in such habitat in the lower Nicola River (Levings and Lauzier, unpubl. data). However, our results show that ponds can also be used by this species, although their relative importance compared with mainstem habitats remains to be assessed in detail. There have been few previously documented reports of juvenile chinook salmon rearing or overwintering in ponds, although hatchery-reared chinook fry stocked into small lakes in south-eastern Alaska grew rapidly and showed a high survival to the smolt stage (Hard 1986). Atlantic salmon (*Salmo salar*) parr have also been found to be abundant in lakes in Newfoundland (Ryan 1986), and it appears that juvenile salmon may utilize ponds, lakes and other standing waters where they form an integral part of the river system, particularly where suitable main-channel habitats are limited. However, biological factors such as competition for food and space may control the species mix in the off-channel habitats, accounting for the relatively low numbers of chinook, rainbow trout, and Dolly Varden char we found in the Coldwater River ponds.

In conclusion, off-channel ponds on the floodplain of the Coldwater River appear to play three major roles in the life cycle of juvenile coho salmon in the river, (1) as an overwintering habitat where fish can avoid severe winter conditions in the main river, (2) as a refuge area where juveniles can shelter from high flows in the main river during summer snowmelt and also possibly avoid predation, and (3) as a summer rearing habitat. Such productive off-channel habitats are likely to be particularly important in low temperature rivers, such as the Cold-

water River, where winter environmental conditions may be major factors limiting the production of juvenile salmonids.

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# Effects of Triploidy on the Swimming Performance of Coho Salmon (*Oncorhynchus kisutch*)

Susan A. Small and D. J. Randall[1]

*Department of Zoology, University of British Columbia, Vancouver, B.C. V6T 2A9*

Small, S. A., and D. J. Randall. 1989. Effects of triploidy on the swimming performance of coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 46: 243–245.

The swimming performance of triploid coho salmon (*Oncorhynchus kisutch*) was compared with diploid controls to assess the ability of these fish to survive if released into the wild. Triploid salmon had similar haematocrits to diploid salmon but they had lower total haemoglobin content in their blood. There was no difference in the maximum sustained swimming ability between triploid and diploid salmon.

On a comparé la performance à la nage de saumons coho (*Oncorhynchus kisutch*) triploïdes à celle de témoins diploïdes pour évaluer l'aptitude de ce poisson à survivre en milieu naturel. Les saumons triploïdes avaient un hématrocrite semblable à celui des saumons diploïdes, mais leur taux d'hémoglobine total était plus bas. Il n'y avait aucune différence entre les triploïdes et les diploïdes au point de vue l'aptitude maximale à la nage prolongée.

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Triploid salmon have been of interest to the aquaculture industry because of the sterility of triploid females (Thorgaard 1983). The energy normally used for gonadal development is allocated wholly for growth and maintenance with obvious benefits to the fish farmer. Sterile fish never lose their silver appearance and high flesh quality and, therefore, have top market value year-round. Sterility also eliminates maturation-induced mortality which is characteristic of the genus *Oncorhynchus*. Triploid males are of no apparent use for aquaculture or release because they mature sexually and are subject to the associated secondary sexual changes. They are also sterile, however, because gonadal development is incomplete (Thorgaard 1983). Triploid female salmon may be useful for release into the wild for stock enhancement if they are few enough in number that they do not compete with wild stock for limited resources and if they do not return to freshwater and interfere with wild-spawning salmon.

Induced triploidy causes increased cell size which could potentially affect a number of physiological processes. There is a 50% increase in chromosome number in nuclei of triploid animals resulting in an approximately proportionate increase in cell size to maintain the nucleo-cytoplasmic ratio (Fankhauser 1941). Associated with an increase in cell size is the reduction in the surface area to volume ratio which is inversely related to the metabolic rate of the cell at the tissue level in certain amphibian species (Monnickendam and Balls 1973; Kamel et al. 1985).

Numerous studies have shown that triploid fish have larger erythrocyte nuclei and overall erythrocyte cell size than diploid fish (Swarup 1959; Cherfas 1966; Cimino 1973; Sezaki et al. 1977; Wolters et al. 1982; Beck and Biggers 1983; Small and Benfey 1987). Triploid and diploid landlocked Atlantic salmon (*Salmo salar*) have equivalent haematocrits (i.e. larger but fewer red blood cells) but triploid salmon have lower total haemoglobin in their blood (Benfey and Sutterlin 1984b). These results suggest that the blood of triploid salmon may have reduced oxygen-carrying capacity. The level of maximum sustained swimming ability ($U_{crit}$) is determined by oxygen delivery to the tissues which in turn is dependent upon maximum cardiac output and blood oxygen-carrying capacity (Jones and Randall 1978). Thus a reduction in blood oxygen-carrying capacity should decrease the level of maximum critical swimming velocity achieved by the fish assuming cardiac output is similar, that is, triploid fish should have a lower maximum $U_{crit}$ than diploid fish, *cetera paribus*. We tested this hypothesis using diploid and triploid coho salmon (*Oncorhynchus kisutch*).

Salmonids are ancestrally polyploid (Schultz 1980; Allendorf and Thorgaard 1984), demonstrating that they are able to coexist with closely related diploid species. An alternate hypothesis might be, therefore, that induced triploidy should have no effect on the aerobic capacity of coho salmon, assuming that aerobic capacity is used as a measure of survival.

## Materials and Methods

### Experimental Fish

The fish used in this study were 14- to 15-mo-old coho salmon. Triploidy was induced by hydrostatic pressure shock (Benfey and Sutterlin 1984a) and the fish were screened for ploidy using propidium iodide flow cytometry (Allen 1983). Triploid and diploid salmon were reared in separate tanks under uniform conditions.

The fish used in the swimming performance test were selected for size due to the size dependency of critical velocity measurements (Jones and Randall 1978). Triploid individuals

[1]Author to whom correspondence should be addressed.

had a mean body wet weight of 15.76 g (SD = 1.24) and a mean fork length of 11.80 cm (SD = 0.31) ($n$ = 7); mean body wet weight and fork length were 15.00 g (SD = 2.55) and 11.84 cm (SD = 0.17) ($n$ = 7), respectively, for diploid salmon. There was no significant difference in body wet weight or fork length between triploid and diploid salmon.

### Haematocrit and Total Haemoglobin Content Measurements

Whole blood was taken from the caudal vein of diploid ($n$ = 6) and triploid ($n$ = 6) salmon by cutting off the tails of freshly sacrificed fish and collecting the blood in heparinized collecting tubes. Total haemoglobin content (Procedure No. 525, Sigma Diagnostics) and duplicate haematocrits for each blood sample were measured. The fish were placed in partitioned black boxes for at least 6 h prior to sampling and were removed individually to reduce the effects of stress on blood composition.

### Swimming Performance

Triploid and diploid salmon were preexercised in separate tanks which were set up to force the fish to swim against a current. The fish were conditioned before measuring their critical velocities to maximize their swimming performance; Farlinger and Beamish (1978) showed that exercise over time increased and haemoglobin content of the blood of largemouth bass (*Micropterus salmoides*) which was reflected in greater critical velocities when compared with unconditioned fish. The fish were fed ad libitum and were exercised for at least 4 wk before swimming performance was measured.

Swimming performance was quantified by measuring the critical swimming velocity of the fish using a Brett respirometer (Brett 1964). In this study, a flow-through rather than a recirculating system was set up so that oxygen saturation of the water would remain fairly constant. The water temperature was 6°C and did not change during the test period. The respirometer was equipped with an electrified grid to prevent the fish from resting on the downstream grid. The water velocity through the fish chamber was calibrated using an Ott small-type current meter (10649), counter f6u (6105), and propeller (10649-4) (A. Ott, Kempton, Bayern).

The body length of each fish, which is equivalent to its fork length in this study, was measured before being placed in the respirometer, where it was allowed to acclimate for 21–24 h with the water set at 1.0 body length per second ($BL \cdot s^{-1}$) which was just fast enough to keep the animal swimming upstream. The electrified grid was turned on (7 V) during the acclimation period to train the fish to swim forward in the chamber. Black plastic was placed over the middle third of the chamber to give the fish a place to hide and a light was shone on the front third to orient the fish. During the test period, the electric grid was turned off and velocity of the water was increased by 0.5 $BL \cdot s^{-1}$ increments every 30 min until the fish was fatigued. Fatigue was defined as the inability of the fish to remove itself from the downstream screen after three consecutive 1-s shocks (9 V) followed by a rapid reduction in water velocity. The critical velocity of the fish, defined as the velocity at which the fish fatigues, was calculated as described by Webb (1971).

At the end of each test period, the animal was removed from the respirometer, weighed, and anaesthetized to take a blood sample by syringe from the caudal vein for ploidy confirmation by flow cytometry.

### Data Analysis

The mean and standard deviation were determined for all measurements taken including body weight and fork length of each fish, haematocrits, blood haemoglobin content, and critical velocities. The significance of the difference between measurements taken on diploid and triploid individuals was determined by single-factor analysis of variance (Ryan et al. 1982).

## Results

Diploid and triploid coho salmon had similar haematocrits, 23.07% (SD = 2.54) and 21.95% (SD = 2.83), respectively ($n$ = 6). The total haemoglobin content of triploid salmon blood (8.45 $g \cdot dL^{-1}$ (SD = 0.61)), however, was significantly less ($p < 0.01$) than that of controls (9.82 $g \cdot dL^{-1}$ (SD = 0.78)). There was no statistically significant difference between the swimming performance of triploid and diploid coho salmon; mean critical swimming velocities ($n$ = 7) were 3.45 $BL \cdot s^{-1}$ (SD = 0.32) and 3.66 $BL \cdot s^{-1}$ (SD = 0.27), respectively.

## Discussion

Erythrocytes and their nuclei are larger in triploid than in diploid coho salmon (Small and Benfey 1987); their haematocrits, however, were similar, which indicates a reduction in the number of red cells in triploid salmon. An important effect on coho blood which was associated with triploidy was the reduction in the total haemoglobin content. Measurements made of whole blood and erythrocyte characteristics in this study are similar to those made for Atlantic salmon (Benfey and Sutterlin 1984b; Graham et al. 1985); however, the difference in haemoglobin content for diploid and triploid coho salmon (14%) was not as great as that found for Atlantic salmon (21–24%) (Benfey and Sutterlin 1984b; Graham et al. 1985). Haematological studies of Atlantic salmon showed that haemoglobin–oxygen affinity and red cell nucleotide triphosphate, an important regulator of haemoglobin–oxygen affinity, are the same for triploid and diploid individuals. The haemoglobin–oxygen loading ratio in triploid Atlantic salmon, however, was found to be only 77% of that found in diploid salmon, and oxygen content of the triploid Atlantic salmon blood was 67% of that observed for Atlantic salmon (Graham et al. 1985). These parameters would probably be comparable in coho salmon based on the similarities in red blood cell size, haematocrit, and total haemoglobin content between coho and Atlantic salmon. However, the reduction in blood oxygen content for triploid coho salmon may not be as great due to the smaller difference in haemoglobin content between triploid and diploid individuals.

There was no significant difference in the swimming performance of the triploid and diploid coho salmon. Several factors associated with triploidy indicated that a lower mean critical swimming velocity would be expected. The reduced oxygen–carrying capacity of triploid salmon blood, due to the lower haemoglobin content and haemoglobin–oxygen loading ratio, should affect the aerobic capacity of the triploid salmon and, consequently, their maximum swimming performance (Jones and Randall 1978). Jones (1971) observed a significant reduction of approximately 33% in the critical velocities for fish whose haematocrits, and therefore haemoglobin content, were experimentally reduced by approximately 44%. Also, the

inverse relationship between cell size and velocity of gas uptake (Holland and Forster 1966) should increase the time required for oxygen to reach the haemoglobin and should slow down oxygen delivery to the muscles. Triploid Atlantic salmon erythrocytes are longer and wider but not thicker than diploid erythrocytes (Benfey and Sutterlin 1984b). The reaction rate for haemoglobin oxygenation is based on the half-thickness of the cell (Holland and Forster 1966) and it is possible that reaction rates would not be hindered by cell size in triploid salmon.

The apparent lack of effect of triploidy on maximum aerobic capacity as examined in this study may be species specific but is consistent with the measurements of resting and active metabolism of diploid and tetraploid treefrogs. The results expected (i.e. a reduction in metabolic rate), based on physiological properties of large cells, are observed at the tissue level but not at the whole animal level (Kamel et al. 1985).

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# Lake Acidification Mitigation Project (LAMP): an Overview of an Ecosystem Perturbation Experiment[1]

D. B. Porcella

*Ecological Studies Program, Electric Power Research Institute, P.O. Box 10412, Palo Alto, CA 94303 USA*

*(J9497)*

It is well known that low-pH waters do not support diverse and highly productive aquatic communities. To restore or maintain fish and other organisms, the quality of these surface waters has been managed by the addition of base materials (limestone, lime, sea shells, and soda ash). This process, liming, commonly involves use of calcitic limestone ($CaCO_3$) to provide basic cations ($Ca^{2+}$) and acid neutralizing capacity (ANC or alkalinity). Limestone is superior to other materials because it neutralizes acidity without causing excessively high or rapidly changing pH levels, provides ANC to buffer future acidity, and increases divalent cations that are physiologically important to fish and that may competitively inhibit the uptake of toxic metal ions. Mitigation of acidic conditions by liming is a proven method for changing chemical conditions in the water, but liming has been applied on a regional management scale only in Sweden (Lessmark and Thornelof 1986). Only sparse ecological data were collected in those applications, and detailed studies of the ecological effects have not been performed. The lake acidification mitigation project (LAMP) was organized to address issues raised as a result of the Swedish and other liming experiences (Fraser et al. 1982; Fares and Kinsman 1984). One objective of LAMP was to learn how aquatic ecosystems respond to the massive chemical perturbation caused by liming and subsequent reacidification. Reacidification following base application is of particular interest because it represents one way to assess the response of lakes to acidification processes. A second objective, not discussed in detail in these papers, was to evaluate practical methods of adding limestone, their costs, efficiency, duration, and effectiveness of treatment.

Generally, experimental design is difficult in ecology and in lake studies specifically because of poor definition of replicates and controls. Lakes represent a continuum of physical, chemical, and biological characteristics that vary in time and space. Consequently, a range of these characteristics was examined to observe how ecological responses to liming vary among lakes. We decided that a minimum of three lakes were needed for manipulation. Because we wanted to view both short-term and long-term ecological effects, the experiment was designed to measure chemical changes over time and space, relate the chemistry to structural and functional responses of lake communities, and then identify the most significant control variables. Specific tasks were to evaluate changes in stocked and unstocked fish populations and other biota in relation to liming and reacidification, the risk of metal toxicity to fish during reacidification after repeated liming, and whether liming protects biota against episodic or littoral zone acidic events.

We chose the Adirondack Mountains for LAMP because acidic deposition is high in the region, and because it contains a number of low alkalinity lakes (Schofield et al. 1985). Based on accessibility, permission to lime, availability of baseline data, ability to perform hydrologic measurements, and chemical and biological characteristics, we selected Cranberry Pond, Woods Lake, and Little Simon Pond. The first two lakes were fishless prior to our studies, whereas Little Simon Pond contained lake trout (*Salvelinus namaycush*). Only older year classes were observed in the lake trout population, so it was probably under stress. The fish community also included brook trout (*Salvelinus fontinalis*) and other fish species. Of the three lakes, Woods is the only one with a substantial pre-LAMP record of study (Goldstein et al. 1985). These three clearwater, drainage lakes provide a range of response times and biological conditions for study of physical and chemical responses to liming and reacidification. As a first approximation to response times, mean hydraulic residence times were 63 d, 174 d, and 450 d for the three lakes, respectively.

The LAMP began field sampling in January 1984. Seventeen months later (May 30–31, 1985) a helicopter limed the two short residence time lakes with a water slurry (71% solids) of fine particle (median diameter 2 μm) calcite (98% calcite) and 0.15% sodium polyacrylate dispersant to aid suspension (Scheffe et al. 1986). Slurry was delivered to the lakes at 6.5 $t \cdot h^{-1}$; about 7 t of dry calcite were added to Cranberry Pond and 23 t to Woods Lake; on a volumetric basis, the liming increased water concentrations of calcite to 34 $mg \cdot L^{-1}$ in Cranberry and 28 $mg \cdot L^{-1}$ in Woods. The slurry was added to obtain uniform concentrations in the water column and uniform areal deposition of a portion of the calcite to the sediments. Four days after chemical perturbation of the two lakes, yearling and fingerling brook trout were introduced to both lakes.

Data collected during the 1–2 yr of observation after the single calcite treatment of these two lakes provide the basis for this series of papers. The long-term ecological effects will be derived from data to be collected on Woods Lake (relimed September 1986) and Little Simon Pond (limed August 1986).

We hypothesized that the spatial and temporal distribution of water entering and exiting the lake along with the chemical composition of those flows would have the greatest effect on in-lake chemical concentrations and mass balances. Therefore, accurate hydrologic characterization of the seasonal and spatial pattern of water inflows was critical to analysis of chemical and biological processes. Staubitz and Zarriello (1989) described

[1]This is part of a series of 13 papers devoted to the Lake Acidification Mitigation Project.

the physical layout of the Cranberry Pond and Woods Lake watersheds, and evaluate the role of groundwater flow paths in relation to surface water flows in these lakes.

Because lake inflows vary on both temporal and spatial scales, we expected to find differences between the chemical responses of the two lakes to liming and reacidification. Fordham and Driscoll (1989) described the transitory effects of limestone addition on water column acid–base chemistry: pH, calcium, and alkalinity. Four weeks after liming, dissolution of calcite had reached 86% in Woods Lake and 79% in Cranberry Pond, based on chemical budgets of calcium ion. By the end of the summer, essentially all the calcite in the two lakes had dissolved; accumulation of calcite particles in bottom sediment was minimal.

As a result of liming, Driscoll et al. (1989a) noted marked reductions in the water column concentrations of aluminum, manganese, and zinc, the only metals significantly above present analytical detection limits for water samples. These reductions occurred over a period of several weeks, leading to metal accumulation in lake bottom sediments, apparently as inorganic mineral precipitates. However, longer-term studies are needed to evaluate the release of these sediment metals when pH is not controlled by the added calcite.

The behavior of chemical variables during reacidification provides a unique opportunity to observe some of the key factors that control acid levels in low ionic strength lakes. Driscoll et al. (1989b) examined chemical trends occurring during reacidification, and compare the role of inflows, outflows, and in-lake processes to account for the loss of alkalinity added during liming.

To further the understanding of water column chemistry, Young et al. (1989) evaluated the role of sediments in the reacidification processes of lakes. This is important not only for estimating the significance of sediment sources of base cations, but for calculating the calcite dose to sediments that would effectively increase the duration of treatment. The sediment exchange of alkalinity components must be quantified if accurate limestone treatments and reacidification times are to be calculated. For example, some of the alkalinity changes in the water column result from sediment–water interchanges. Another important issue is whether settled undissolved calcite can be easily quantified in sediments. These concerns become quantitatively important errors if neglected when calculating mass balances of limed systems.

The physical and chemical variables discussed to this point fit easily into a modeling framework. Using a lumped parameter dynamic model, DePinto et al. (1989) evaluated the importance of inflow, sediment interactions with water, seasonal effects, and other variables that affect the duration of treatment. They demonstrate the model's capability for predicting the effect of sediment calcite treatment on the water column reacidification rate when hydrologic variables are known.

Clearly, a large integrated study of ecological effects requires both detailed physical, chemical, and biological measurements and the integration of these measurements into some cohesive whole. Although LAMP does not apply a formal modeling structure for the biotic components, the concept of food webs in relation to physical and chemical variables provides the underpinning for the different biological papers.

Bukaveckas (1989) discussed phytoplankton dynamics during liming and reacidification in Cranberry and Woods as affected by light, temperature, and chemical variables. Immediately after liming, carbon dioxide ($CO_2$) appears to be limiting due to the high pH values caused by the rapid dissolution of calcite ($CaCO_3$). Over a longer term, nutrients do not appear to play a major role in phytoplankton dynamics because nitrogen and inorganic carbon compounds appear not to be limiting in the lakes, and only low concentrations of phosphorus occur which seem to be unaffected by the lake liming or reacidification. In a related study separate from LAMP, Roberts and Boylen (1989) studied sediment algae along a depth gradient and found responses to liming consistent with phytoplankton responses: diatom composition but not biomass changed; deep station cyanobacteria biomass decreased after liming but the distinct depth zonation patterns did not change.

Without a modeling perspective, the zooplankton responses to liming and species shifts of food organisms and predators cannot easily be deciphered. Schaffner (1989) attributed zooplankton responses to phytoplankton changes and fish stocking effects that could cause changes in both zooplankton production and loss terms. Evans (1989) characterized the macroinvertebrate fauna prior to liming which forms the initial base of the food supply for the stocked trout. The combination of zooplankton and macroinvertebrate data provide the initial conditions for parameterizing a bioenergetics model to explore food chain limitations on trout production.

Although producer–grazer populations were not subjected to experimental manipulations, stocking provided the opportunity for experiments with different strains and life stages of brook trout and for testing simple fish production models used for evaluating food chain relationships. Gloss et al. (1989) described results of stocking experiments with different life stages using growth and survival as indices of success, and the effects of fish on invertebrates as reflected in diet. Schofield et al. (1989) used a bioenergetics model based on diet analysis to compare actual versus estimated production to test whether liming is a suitable management technique for maintaining adequate recruitment and growth. Consequently, they test the hypothesis that the effects of predation-induced changes in prey community structure substantially affects the production efficiency of stocked trout populations.

During the studies summarized in this volume, no deleterious effects of liming were observed. The observed changes in community struture are desirable and result from water quality changes and stocking of trout. Apparently, nutrients or other factors limit production of the fish community of the limed lakes because productivity does not differ significantly from otherwise similar circumneutral lakes. Hydrologic and in-lake processes control reacidification and precise predictions of when to relime can be made so as to maintain water quality that will support aquatic communities typical of circumneutral lakes. The major uncertainty in forecasting arises from hydrologic variation. Although liming enhances metal sequestration within lakes, long-term study will evaluate whether reacidification will remobilize the metals in lake sediments. Similarly, long-term research is necessary to evaluate whether model predictions of bulk water chemistry variables are protective of biota, especially during spatial or temporal episodic acidification events. Likewise, the effects of changes in prey density caused by the interaction of liming and predation by the reintroduced fishery may cause changes that could not be predicted from the short-term measurements discussed in this series of papers. These questions are under investigation during the current research to measure long-term ecological responses to calcite addition to lakes.

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# Short-Term Changes in the Chemistry of Trace Metals Following Calcium Carbonate Treatment of Acidic Lakes[1]

Charles T. Driscoll, Gerald F. Fordham, William A. Ayling, and Leah M. Oliver

*Department of Civil Engineering, Syracuse University, Syracuse, NY 13244, USA*

Driscoll, C. T., G. F. Fordham, W. A. Ayling, and L. M. Oliver. 1989. Short-term changes in the chemistry of trace metals following calcium carbonate treatment of acidic lakes. Can. J. Fish. Aquat. Sci. 46: 249–257.

Marked changes were evident in the concentrations of trace metals (aluminum, manganese, and zinc) following base application to two acidic lakes in the Adirondack region of New York. Immediately after calcite treatment, epilimnitic pH values increased above 9.0. This response coincided with a shift in the speciation of aluminum from acid-soluble to labile (inorganic) monomeric forms. Following the manipulation, pH values decreased below 8.0 as the epilimnion equilibrated with atmospheric $CO_2$. Within 1–2 mo, aluminum, manganese, and zinc concentrations were greatly reduced, typically by an order of magnitude. The mechanism(s) for immobilization of trace metals following base treatment is not entirely clear. However, chemical equilibrium calculations suggest that at the higher pH resulting from base addition, lake water was oversaturated with readily forming aluminum and manganese minerals. Therefore, removal of these metals from the water column may have been due to direct precipitation. Solutions were highly undersaturated with zinc minerals, so zinc retention probably occurred by adsorption or coprecipitation reactions. Acidic Adirondack Lakes are generally net sinks for aluminum, and conservative with respect to transport of manganese and zinc. Base addition greatly enhanced retention of all three metals.

On a constaté que la concentration de divers métaux présents à l'état de traces (aluminium, manganèse et zinc) avait changé de façon marquée après l'application d'une base dans deux lacs acidifiés des Adirondacks, dans l'État de New York. Immédiatement après le traitement à la calcite, le pH de l'épilimnion est monté au-dessus de 9,0. Ce phénomène a coïncidé avec un changement des espèces de l'aluminium qui, de formes solubles dans l'acide, sont passées à des formes monomères labiles (inorganiques). Après le traitement, le pH a baissé sous 8,0, alors que s'établissait un équilibre entre l'épilimnion et le $CO_2$ atmosphérique. En l'espace d'un ou deux mois, les concentrations d'aluminium, de manganèse et de zinc avaient baissé considérablement, généralement d'un ordre de grandeur. Le mécanisme régissant la rétention des métaux en traces après l'application de la base n'est pas entièrement compris. Toutefois, d'après les calculs basés sur des conditions d'équilibre chimique, on constate qu'au pH relevé par l'application de la base, l'eau du lac était sursaturée en minéraux d'aluminium et de manganèse à formation rapide. Il se peut donc que la disparition de ces métaux de la colonne d'eau ait été due à la précipitation directe. Comme les solutions étaient très loin d'être saturées en minéraux de zinc, il est probable que le zinc a été retenu à cause d'un phénomène d'adsorption ou de réaction de co-précipitation. Les lacs acidifiés ont généralement un effet net de captage de l'aluminium et de conservation quant au transport du manganèse et du zinc. Avec l'application de la base, la rétention de ces trois métaux s'est considérablement accrue.

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An important consequence of surface-water acidification is the increase in trace metal concentrations that coincides with decreases in pH (Baker 1982; LaZerte 1986). Research on trace metal leaching resulting from acidification has largely focused on the chemistry and speciation of aluminum due to its (1) role in the pH buffering of acidic waters (Dickson 1978; Driscoll and Bisogni 1984), (2) interactions with critical elements such as phosphorus and dissolved organic carbon (Dickson 1978; Effler et al. 1985), and (3) potential toxicity to aquatic organisms (Driscoll et al. 1980; Baker and Schofield 1982). Elevated concentrations of other trace metals, including copper, cadmium, lead, nickel, zinc, and manganese, have also been reported in acid-impacted lakes in Europe and North America (Henriksen and Wright 1978; Dillon et al. 1979; Dickson 1980; Baker 1982) and these conditions may have deleterious effects on water quality.

Direct application of base is one approach that has been used to mitigate surface-water acidification (Bengtsson et al. 1980; Porcella 1989). Over the longer term (months to years), base treatment has been shown to increase pH, decrease trace metal concentrations, and improve the biological diversity of lake systems (Hultberg and Andersson 1982; Wright 1985). Although research has generally provided a good understanding of the longer-term changes in chemistry and biology in base-treated waters, there is a lack of detailed information on the physical and chemical response of lake systems immediately succeeding chemical manipulation. This limitation in our knowledge has hindered assessments of short-term biological effects following base amendment to acidic lakes.

[1]This is part of a series of 13 papers devoted to the Lake Acidification Mitigation Project.

In this investigation we evaluate changes in the chemistry of aluminum, manganese, and zinc with two acidic lakes immediately after calcium carbonate treatment. Through this effort we hoped to quantify the persistence of trace metals within the water column of base-amended lakes and further assess the processes regulating the immobilization of these metals. This study was a subcomponent of the Lake Acidification Mitigation Project (LAMP), which is a multidisciplinary investigation of ecosystem and process-level questions concerning the response of acidic lakes to base amendment (see Porcella 1989).

## Study Site and Experimental Methods

This investigation was conducted at two lakes in the Adirondack region of New York, Woods Lake (43°52′N, 74°58′W) and Cranberry Pond (43°51′N, 74°58′W). The surrounding watersheds are characterized by shallow glacial till and highly acidic soils (April and Newton 1985; Staubitz and Zarriello 1989). Moreover, the catchments are forested with largely deciduous vegetation. Woods Lake and Cranberry Pond are small lakes with maximum depths of 11.5 and 6.5 m, respectively, and mean hydraulic residence times of 174 and 63 d, respectively (see Staubitz and Zarriello 1989).

These lakes have been previously characterized chemically (Schofield et al. 1985; Driscoll et al. 1989). The water quality of both sites is typical of chronically acidic lakes in the Adirondack region of New York (Driscoll and Newton 1985; Schofield et al. 1985). Prior to the manipulation, sulfate was the dominant anion in the solution chemistry of both lakes. Moreover, the sum of strong acid anions (sulfate, nitrate, and chloride) generally exceeded the sum of basic cations (calcium, magnesium, potassium, and sodium) on an equivalence basis, coinciding with highly acidic water quality (pH values generally less than 5.0).

Woods Lake and Cranberry Pond were treated on 30 and 31 May 1985 by slurry application of 22.6 and 7.2 t (dry basis), respectively, of fine-powder, high-purity calcium carbonate. Sodium polyacrylate (0.15%) was used in the slurry as a surfactant, facilitating the suspension of calcite, and ultimately promoting dispersion and wetting when the material was released to the water column. A discussion of the base application to the two lakes is provided in Porcella (1989).

Samples were collected for water chemistry analysis at the inlets, outlet, and with depth (0,1,2,4,6,8,10, and 11 m in Woods Lake; 0,2,4, and 6 m in Cranberry Pond) from a water column station at each lake. Sites were monitored nominally at 3-wk intervals, with weekly samples during spring snowmelt. In addition, an intensive sampling program was implemented immediately following the manipulation. Water column and lake outlet collections were made 1,2,6,10,20, and 25 d after calcium carbonate application. Water column samples were collected with a 4-L Kemmerer sampler.

Immediately after collection, samples were transported to the field station for the measurement of pH and dissolved oxygen, filtration for the determination of suspended solids and processing for analysis of monomeric aluminum fractions. Following activities at the field station, samples were shipped to Syracuse University for analysis. Immediately upon receipt at Syracuse University (generally within 72 h of collection), samples were analyzed for dissolved organic carbon (DOC). Samples were stored at 4°C until the remainder of the analyses were completed, typically within 1 mo after collection. Water samples were analyzed for all major solutes using methods detailed in Fordham and Driscoll (1989). A summary of the parameters monitored and analytical methods relevant to the trace metal chemistry are provided in Table 1.

An important component of this phase of the study was an evaluation of changes in the concentration and speciation of aluminum in the water column following base application. In order to better understand the chemistry and availability of aluminum, samples were fractionated into various forms using the method developed by Driscoll (1984). In this procedure nonlabile monomeric aluminum is measured directly and is considered to represent organic complexes of aluminum. Labile monomeric aluminum is determined as monomeric aluminum less nonlabile monomeric aluminum. This fraction is an estimate of inorganic species of monomeric aluminum, including aquo, hydroxide, fluoride, and sulfate complexes. Acid-soluble aluminum is total aluminum less monomeric aluminum and is thought to represent particulate aluminum or aluminum that requires acid digestion for detection.

Using water chemistry data collected from the LAMP, mineral phase solubility saturation indices (*SI*) were calculated.

$$SI = \log (Qp/Kp),$$

where *Qp* is the ion activity product of solutions and *Kp* is the thermodynamic solubility product of the mineral phase of interest. Negative values of *SI* indicate conditions of undersaturation with respect to mineral phase solubility, while positive values suggest oversaturation. During oversaturation there is potential

TABLE 1. Procedures used in the analysis of lake water samples.

| Parameter | Method | Reference |
|---|---|---|
| pH | Potentiometrically glass electrode | |
| Dissolved organic carbon (DOC) | UV enhanced persulfate digestion, IR detection of $CO_2$ | Dohrmann 1984 |
| Dissolved oxygen | Winkler titration | APHA 1985 |
| Total Al | Al digestion (1 h, pH 1), 8-hydroxyquinoline extraction into methyl isobutyl ketone (MIBK), analysis by atomic absorption spectrophotometry (AAS), graphite furnace | Barnes 1976, Driscoll 1984 |
| Monomeric Al | Field extraction by 8-hydroxyquinoline into MIBK, analysis by AAS, graphite furnace | Barnes 1976, Driscoll 1984 |
| Nonlabile monomeric Al | Fractionation by ion exchange column, analysis for monomeric Al | Driscoll 1984 |
| Total Mn, Zn | Acid digestion (pH 1), analysis by AAS, graphite furnace | APHA 1985 |

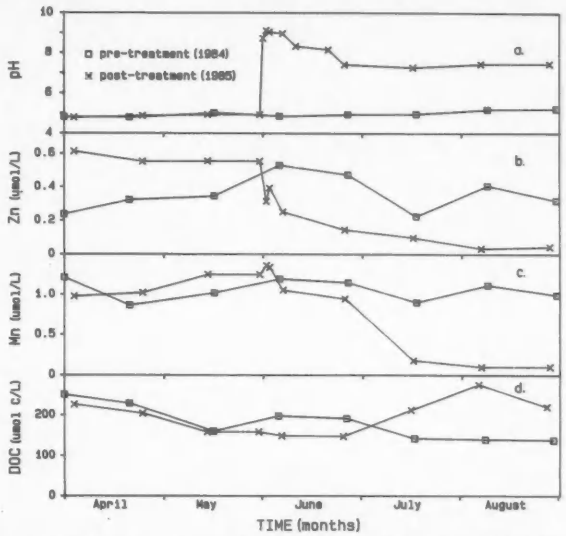


FIG. 1. Upper water (above 6 m) volume-weighted values of (a) pH, (b) zinc, (c) manganese, and (d) dissolved organic carbon (DOC) prior to and following base treatment of Woods Lake (on 30, 31 May 1985).

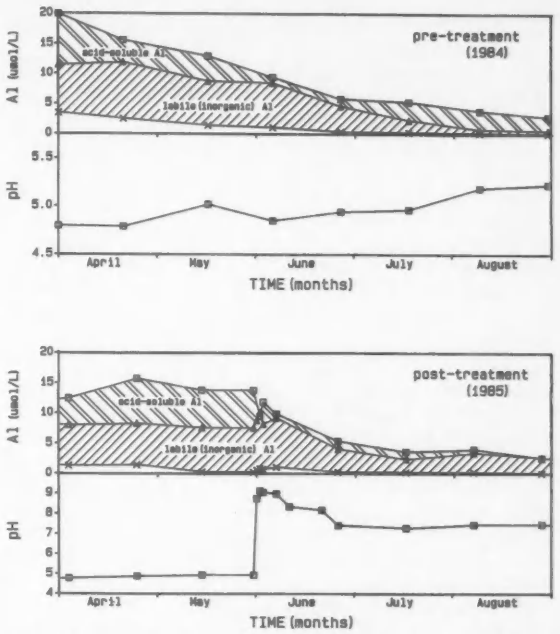


FIG. 2. Dissolved organic carbon (DOC) isopleth of Wood Lake prior to and following base addition. Base treatment occurred on 30, 31 May 1985.

for in-lake formation of metal hydrolysis products and direct precipitation of particulate mineral phases.

Concentrations of labile (inorganic) monomeric aluminum, pH, and inorganic complexing ligands (fluoride, sulfate) were used as input parameters in the chemical equilibrium model ALCHEMI (Schecher and Driscoll 1987, 1988) to determine the *SI* values with respect to aluminum mineral phase equilibrium. Water column concentrations of manganese and zinc, together with pH and major solute concentrations were used to calculate *SI* values for manganese and zinc minerals with the chemical equilibrium model MINEQL (Westall et al. 1976). Thermodynamic calculations were corrected for variations in temperature and ionic strength.

Water column chemistry was evaluated with regard to the solubility of mineral phases. We selected natural gibbsite ($\log^* K_{so} = 8.77$; May et al. 1979) as a reference mineral for *SI* calculations of aluminum solubility because acidic waters in the northeastern United States closely follow predicted equilibrium (Johnson et al. 1981; Driscoll et al. 1984; Cronan et al. 1986). However, aluminum concentrations may be regulated by a number of hydroxide solid phases ranging from relatively insoluble synthetic gibbsite ($\log^* K_{so} = 8.11$; May et al. 1979) to relatively soluble microcrystalline ($\log^* K_{so} = 9.35$; Hem and Roberson 1967) or amorphous aluminum hydroxide ($\log^* K_{so} = 10.8$; Stumm and Morgan 1970). Manganese concentrations have been shown to be similar to values predicted by manganite solubility ($\log^* K_{so} = 25.27$; Linsay 1979) in an Adirondack lake (White and Driscoll 1987a), so this phase was used as a reference mineral. A number of solid phases may potentially regulate zinc solubility, including: smithsonite ($\log^* K_{so} = -10.00$; Smith and Martell 1976), hydrozincite ($\log^* K_{so} = 9.65$; Sillen and Martell 1964), and a range of zinc hydroxide phases ($\log^* K_{so} = 11.5$ to 12.45; Ball et al. 1980). A detailed description of the uncertainty associated with thermodynamic calculations involving aluminum is available in Schecher and Driscoll (1987, 1988). Thermodynamic data used in chemical

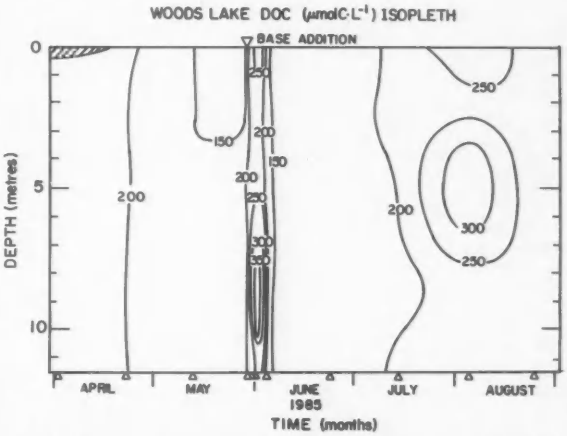


FIG. 3. Upper water (above 6 m) volume-weighted concentrations of nonlabile (organic) monomeric aluminum (*x*), labile (inorganic) monomeric aluminum, acid-soluble aluminum, and pH prior to and following base treatment of Woods Lake (on 30, 31 May 1985).

equilibrium calculations involving manganese and zinc are summarized in Ball et al. (1980).

## Results and Discussion

### General Chemical Characteristics

Pronounced changes in water quality were evident in Woods Lake and Cranberry Pond following base application. The short-term response of both lakes to base application was very similar (Fordham and Driscoll 1989; Driscoll et al. 1989). Woods Lake

(11.5 m) is deeper than Cranberry Pond (6.5 m) and more effectively shows patterns resulting from thermal stratification, consequently this discussion will largely be illustrated using data from Woods Lake. A detailed description of the acid/base chemistry of these lakes following the manipulation is provided in Fordham and Driscoll (1989). Briefly, the water column pH of both lakes increased from below 5 before treatment to above 9 immediately after the calcium carbonate application, coinciding with increases in dissolved calcium, acid neutralizing capacity (ANC), and dissolved inorganic carbon (DIC) (Fordham and Driscoll 1989, Fig. 4). This marked shift in pH was attributed to the relatively low concentrations of DIC in the water column, which provided little buffer capacity against the addition of base. At the time of application, Woods Lake was thermally stratified, with a thermocline at 8 m depth. Apparently the calcium carbonate particle size was small enough (median diameter 2 μm) that significant penetration through the thermocline did not occur. As a result, the treatment was largely restricted to the upper mixed waters and acidic (pH $< 6.0$) conditions persisted below the thermocline throughout summer stratification until turnover. Within a few weeks following treatment, marked increases in water column DIC were evident due to atmospheric invasion of $CO_2$. Inputs of $CO_2$ served to depress pH values in the epilimnion below 8.0. Once equilibrium with atmospheric $CO_2$ was attained, the epilimnion remained at near neutral conditions for the summer period after base addition.

In addition to these changes in acid/base chemistry, other transformations in water quality were evident following base application. For example, pulsed increases in DOC were observed at the water surface and lake outlets (Fig. 1,2) shortly (2–6 d) after the treatment. Some of this increase could, undoubtedly, be attributed to the sodium polyacrylate surfactant present in the calcium carbonate slurry applied to the lakes. A peak in DOC was also evident above the thermocline of Woods Lake within a few days following treatment. Although the source of this latter DOC increase is not apparent, the lysing and sedimentation of phytoplankton from the water column during treatment may have contributed (Bukaveckas 1989). Within a week following the calcium carbonate addition, DOC decreased to the lowest concentrations during the study period (Fig. 1,2). Short-term reductions in DOC as a consequence of base application have been previously reported (Driscoll et al. 1982) and attributed to pH dependent decreases in the solubility of humic substances (SNFB 1981; Hultberg and Andersson 1982) and/or coagulation of dissolved organic substances with hydrolyzing metals (Effler et al. 1985).

Later in the summer (2 mo after treatment), DOC concentrations increased to approximately 50% above values observed the previous year (Fig. 1,2). Several investigators have observed increases in lake DOC following calcite treatment (Dickson 1979; Wright 1985), which might be due to phytoplankton or sediment release. Most researchers, however, have indicated that increases in DOC cannot be explained by changes in phytoplankton biomass (Dillion et al. 1979; Yan 1983; Wright 1985). In our study, water column concentrations of DOC show a middepth maximum in August (Fig. 2). This pattern appears to follow a peak in chlorophyll above the thermocline in late July (Bukavakas 1989) and probably would not be expected from sediment release.

Woods Lake and Cranberry Pond were well oxygenated (Driscoll et al. 1989). Some depletion of oxygen was evident in Woods Lake below the thermocline, but concentrations were

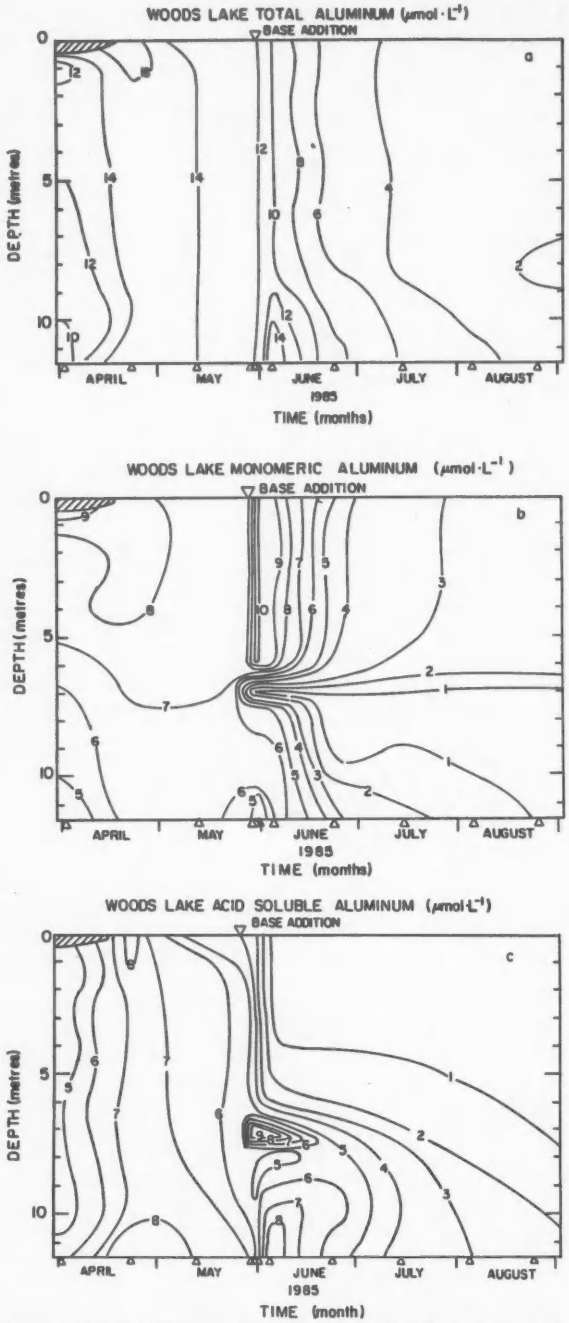


FIG. 4. Isopleth of (a) total aluminum, (b) monomeric aluminum, and (c) acid soluble aluminum concentrations in Woods Lake prior to and following base addition. Base manipulation occurred 30, 31 May 1985.

generally above 100 μmol·L. The treatment did not appear to have a direct effect on oxygen concentrations. However, acid neutralization coincided with conditions of stronger thermal stratification (Driscoll et al. 1989). Increased deposition of organic matter to the hypolimnion coupled with stronger

thermal stratification may have contributed to oxygen reduction in the lower waters.

### Trace Metal Chemistry

Changes in trace metal concentrations, consistent with increases in pH and pH-dependent metal solubility, were evident following base application. Within a few weeks after treatment, epilimnetic concentrations of total aluminum (Fig. 3), manganese, and zinc (Fig. 1) decreased by approximately one order of magnitude. In this study concentrations of total manganese and zinc were monitored, rather than dissolved (filtered) values. Previous studies of manganese and zinc chemistry in an adjacent acidic lake (Dart's Lake, a LAMP reference lake) have shown that water column concentrations of these metals are predominately in a filterable form (White and Driscoll 1987a, 1987b). Like most acidic Adirondack lakes, concentrations of suspended solids in Woods Lake (1.5 ± 3.5 mg·L prior to manipulation and 1.2 ± 0.9 mg·L following treatment) and Cranberry Pond (1.0 ± 0.9 mg·L prior to application and 1.1 ± 1.0 mg·L after neutralization) were very low throughout the study period. As a result, particulate metal concentrations would be expected to be low. Moreover, selected samples were analyzed to ensure that total concentrations of manganese and zinc were largely equal to dissolved values (by filtration with a 0.1-μm pore diameter polycarbonate filter). Data suggest that particulate concentrations of manganese and zinc were only significant just above the thermocline for a short period following base application. For this study, total concentrations of manganese and zinc appeared to be a good estimate of dissolved values.

### Aluminum Chemistry

Acidic Adirondack lakes, including Woods Lake and Cranberry Pond prior to treatment, typically show decreases in aluminum concentrations during the summer stratification (Fig. 3), Driscoll and Schafran 1984; Schofield et al. 1985; Schafran and Driscoll 1987). This pattern has been attributed to reduced inlet concentrations as well as in-lake generation of ANC, largely due to nitrate reduction (Driscoll and Schafran 1984; Schofield et al. 1985; Schafran and Driscoll 1987). Concentrations of total aluminum showed little change in Woods Lake and slightly increased in Cranberry Pond immediately after base application (Fig. 3). Throughout the summer season following treatment, total aluminum concentrations slowly decreased (Fig. 4). It is difficult to discern any difference in total aluminum concentrations in these lakes between pretreatment and posttreatment years.

Although variations in total aluminum were subtle, changes in aluminum speciation were dramatic. Prior to treatment, water column aluminum was predominantly in the labile (inorganic) monomeric fraction, with significant concentrations of acid soluble aluminum (Fig. 3). Concentrations of nonlabile (organic) monomeric aluminum were very low and consistent with low concentrations of DOC. Immediately following base application, a marked shift from acid-soluble to monomeric aluminum occurred in both lakes (Fig. 4b,c). This increase in monomeric aluminum largely occurred through increases in the labile (inorganic) monomeric fraction. Slight increases in nonlabile (organic) monomeric aluminum were also observed. However, these increases were small relative to the overall changes in aluminum chemistry and the nonlabile (organic) monomeric fraction remained a small percentage of total water column alu-

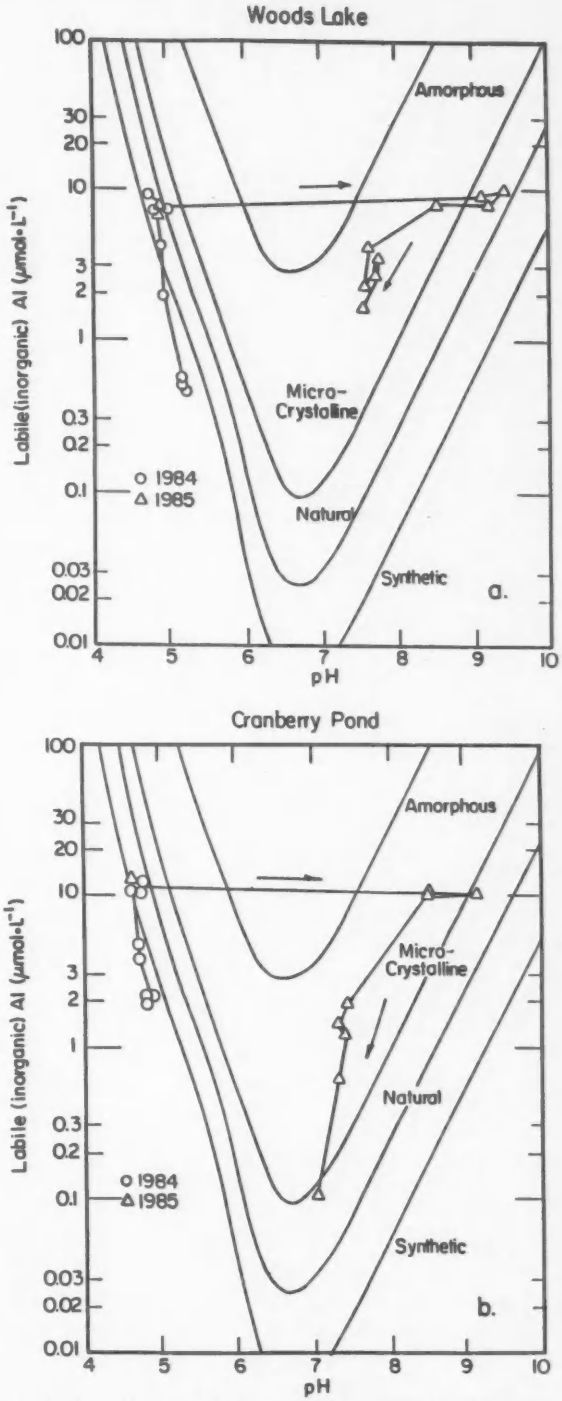


FIG. 5. Concentrations of labile (inorganic) monomeric aluminum as a function of pH in (a) Woods Lake and (b) Cranberry Pond. Changes in aluminum–pH relationships prior to and following base application are indicated by arrows. Superimposed on this figure are the theoretical solubility of synthetic, natural, microcrystalline, and amorphous aluminum hydroxide mineral phases.

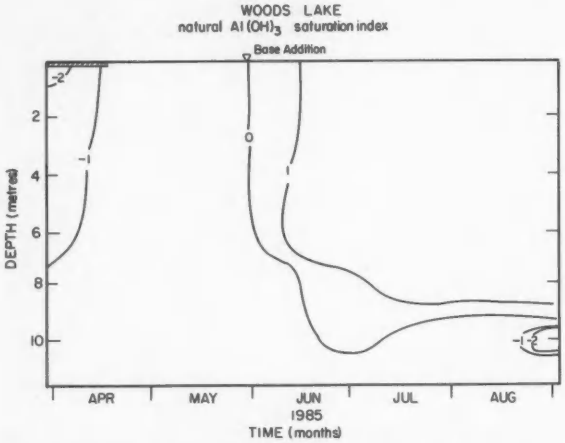


FIG. 6. Saturation index (*SI*) isopleth of Woods Lake with respect to the solubility of natural gibbsite ($\log^*K_{so} = 8.77$) prior to and following base addition. Base treatment occurred on 30, 31 May 1985.

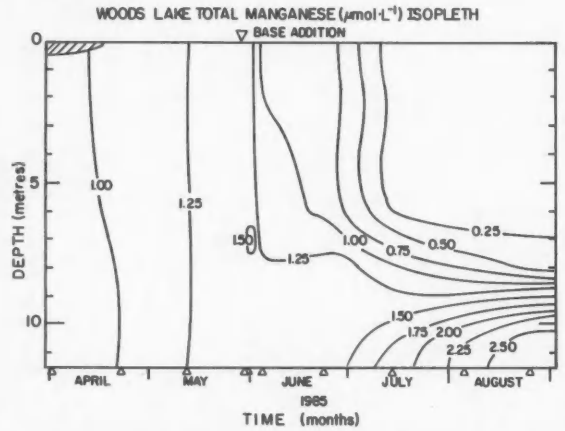


FIG. 7. Isopleth of manganese concentrations in Woods Lake prior to and following base addition (on 30, 31 May 1985).

minum. It is well established that the solubility of inorganic aluminum increases with increases in pH above values of 6.0 (Stumm and Morgan 1970). The observed increases in labile (inorganic) monomeric aluminum appeared to be qualitatively consistent with the pH-dependent solubility of aluminum minerals. Above the thermocline, an accumulation of acid soluble aluminum was evident for several weeks following base addition (Fig. 4c). This particulate aluminum may have been the result of sorption on calcite and other suspended particles. Just above the thermocline, concentrations of monomeric aluminum were extremely low. The high acid-soluble aluminum concentrations and low concentrations of labile (inorganic) monomeric aluminum are consistent with the low solubility of aluminum minerals in the pH range 7.0 – 8.0.

Prior to the manipulation, there was concern that addition of the polyacrylate surfactant might act to mobilize trace metals, particularly aluminum, through complexation reactions. Fortunately no evidence to support this concern was observed, as the speciation of aluminum did not shift toward increased concentrations of the nonlabile (organic) monomeric fraction in response to the increase in DOC at the surface of the lakes.

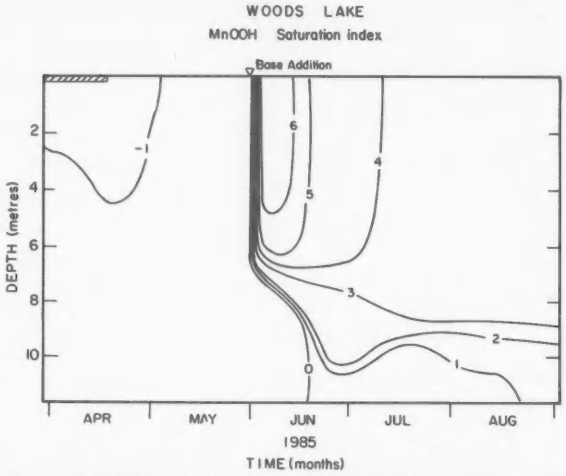


FIG. 8. Saturation index (*SI*) isopleth of Woods Lake with respect to manganite solubility ($\log^*K_{so} = 25.27$) prior to and following base addition. Calcite manipulation occurred on 30, 31 May 1985.

During the months following base application, a systematic decline in upper water concentrations of monomeric aluminum (largely the labile (inorganic) monomeric fraction) occurred, coinciding with decreases in pH (Fig. 4b). Monomeric aluminum concentrations remained extremely low in the layer of water just above the thermocline. Concentrations of acid-soluble aluminum declined throughout the water column, suggesting that over time this material was transported to the lake sediments or out the lake outlet. Decreases in total and monomeric aluminum concentrations were also observed in the lower waters over the summer season (Fig. 4b,c). While these hypolimnetic changes were consistent with modest increases in pH, they are probably not directly attributable to calcite addition. Rather, increases in the ANC of the lower waters coincided with in-lake reduction processes, as evidenced by nitrate depletion, and enrichment of ammonium, iron, and manganese concentrations. Moreover, increased concentrations of calcium were not observed in the hypolimnion during the stratification period following treatment (Fordham and Driscoll 1989).

Although patterns of aluminum solubility were qualitatively consistent with the theoretical pH-dependent solubility of mineral phases, conditions of disequilibrium were apparent. Prior to base treatment, Woods Lake and Cranberry Pond were highly acidic and near saturation with respect to the solubility of natural and synthetic gibbsite (Fig. 5,6). Thermodynamic calculations using the chemical equilibrium model ALCHEMI show that before the manipulation labile (inorganic) monomeric aluminum was largely in an aquo form. During acidic winter conditions, waters were generally undersaturated with respect to the solubility of synthetic and natural gibbsite, while during the higher pH, summer season, solutions approached and sometimes exceeded the solublity of these mineral phases. The increase of ANC and pH due to calcite addition caused virtually complete hydrolysis of aluminum in the upper mixed waters, as chemical equilibrium calculations using ALCHEMI indicated that labile (inorganic) monomeric aluminum was predominately present as the species $Al(OH)_4^-$. This increase in pH caused solutions to shift to the alkaline edge of mineral phase

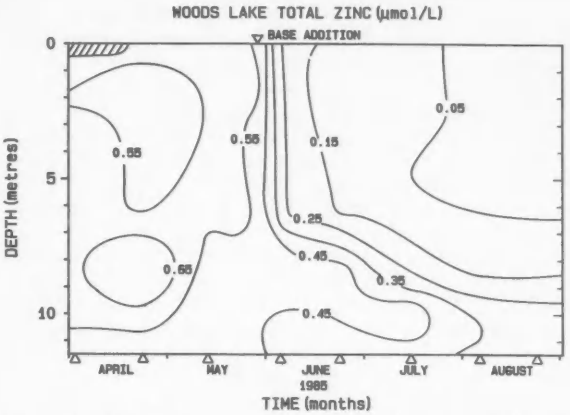


FIG. 9. Isopleth of zinc concentrations in Woods Lake prior to and following base addition. Calcite treatment occurred on 30, 31 May 1985.

solubility (Fig. 5). The epilimnetic waters exhibited high $Al(OH)_3$ *SI* values following the manipulation, generally exceeding the solubility of natural gibbsite. The lower, untreated hypolimnion remained acidic and was undersaturated with respect to the solubility of natural gibbsite (Fig. 6). As the base treated waters equilibrated with atmospheric $CO_2$, pH values decreased to below 8.0 and concentrations of labile (monomeric) aluminum decreased. Measured concentrations did not, however, follow values predicted from mineral phase solubility. Rather, the epilimnetic waters became highly oversaturated with respect to the solubility of natural and microcrystalline gibbsite. In the more rapidly reacidifying Cranberry Pond, as pH decreased aluminum concentrations approached values predicted from the solubility of natural gibbsite. In both lakes several months were required to reestablish apparent equilibrium with aluminum hydroxide solubility.

## Manganese Chemistry

Like monomeric aluminum, slight increases in manganese concentrations were observed in the epilimnion and outlet waters immediately following base application (Fig. 1). Within a month after the manipulation, manganese concentrations began to decrease significantly in the upper mixed waters and lake outlets. By the end of the summer stratification period, epilimnetic concentrations decreased to low values. A marked gradient in total manganese was evident from just above the thermocline to the lower depths of the lakes (Fig. 7). This pattern was qualitatively consistent with the relatively low solubility of manganese in the high (neutral) pH, well oxygenated, upper waters and the considerably higher solubility in the acidic, reducing, lower waters.

Lake pool calculations indicate that although there was a marked depletion of manganese in the upper mixed waters, this decline was offset by increased concentrations in the hypolimnion. It is entirely possible that deposition of manganese from the upper mixed waters was to some extent remobilized due to reducing conditions in the lower waters or, more likely, within the sediments.

Like aluminum, concentrations of manganese did not precisely follow theoretical values predicted from mineral phase solubility (Fig. 8). Before the manipulation, water columns were generally undersaturated with respect to the solubility of manganite. Immediately after calcite treatment, the epilimnetic waters of Woods Lake and Cranberry Pond were highly oversaturated with respect to the solubility of manganite (*SI* > 6.0). Over the summer stratification period, *SI* values decreased considerably, although solutions remained highly oversaturated. Within the hypolimnion, solutions were also somewhat oversaturated with respect to the solubility of manganite, although not as highly oversaturated as the epilimnetic waters. Conditions of oversaturation with respect to manganite solubility were also reported by White and Driscoll (1987a) for the hypolimnion of acidic Dart's Lake. These authors attributed this pattern to reducing conditions within the sediments followed by mobilization of $Mn^{2+}$ to the water column. The relatively slow kinetics of $Mn^{2+}$-oxidation at low pH values (Stumm and Morgan 1970) allow conditions of oversaturation to persist for extended periods. Since the lower waters of Woods Lake and Cranberry Pond were oversaturated with respect to manganite solublity, it would appear that after oxidation and hydrolysis in the upper waters, manganese was deposited to the sediments. Under reducing conditions in the sediments, manganese was resolubilized and transported upward to the hypolimnion.

## Zinc Chemistry

Concentrations of zinc were elevated in both lakes prior to treatment (Fig. 1,9). After base application, zinc was readily depleted in the upper mixed waters. By late July, concentrations decreased by approximately an order of magnitude from pretreatment values. High concentrations of zinc persisted below the thermocline due to acidic conditions in this region of the lake. Within the hypolimnion, concentrations of zinc eventually decreased later during summer stratification, coinciding with increases in pH. However, hypolimnetic concentrations of zinc were considerably higher than values in the upper waters throughout the stratification period following base application.

Concentrations of zinc were undersaturated with respect to the solubility of all mineral phases examined, both before and after the manipulation. Thermodynamic calculations indicate *SI* values below $-3.0$ for all zinc minerals considered. Therefore, unlike aluminum and manganese, it is doubtful that immobilization of zinc occurred by direct precipitation. Several investigators have shown that zinc is strongly adsorbed to particulate matter at pH values above 6.0 (Kinniburgh and Jackson 1981; Millward and Moore 1982). It is probably reasonable to suggest that retention of zinc occurred by adsorption on particles and/or coprecipitation with hydrolyzing metals or organic matter that was facilitated under the high pH conditions following base application.

## General Discussion of Trace Metal Chemistry

There is considerable information in the literature on the chemistry of trace metals in acidic lakes. In general, concentrations of aluminum, manganese, and zinc are elevated in acidic surface waters (Baker 1982). Nilsson (1985) reported that in Sweden, acidic Lake Gardsjon was a net sink for terrestrial inputs of aluminum and a net source of manganese. In a review of trace metal transformations, LaZerte (1986) concluded that acidic lakes were generally net sinks for trace metals, however trace metal transport was more conservative in acidic lakes than in circumneutral lakes. From lake enclosure experiments conducted at the Experimental Lakes Area in Ontario, Canada, Santschi et al. (1986) observed marked removal of tracers $^{54}Mn$

and $^{65}Zn$ through adsorption on particles at water column pH 6.5–7.0. When enclosures were subsequently acidified to pH 4.8 these metals were remobilized from sediments to the water column. Schindler et al. (1980) also reported sediment release of aluminum, manganese, and zinc, and enhanced trace metal mobility following acidification of lake enclosures.

There has been considerable research on the chemistry and transport of trace metals in a LAMP reference lake, Dart's Lake (Driscoll and Schafran 1984; White and Driscoll 1985, 1987a, 1987b; Schafran and Driscoll 1987). In this acidic lake, inputs of aluminum were retained during the low flow summer period and this pattern was consistent with conditions of oversaturation with respect to the solubility of aluminum hydroxide. Moreover, Dart's Lake was conservative with respect to inputs of manganese and zinc, as no net retention/release was evident.

The base treatment of Woods Lake and Cranberry Pond profoundly altered trace metal behavior. Water column concentrations of aluminum, manganese, and zinc were greatly reduced following calcite application. This response, however, was not immediate. Rather, a period of 6–8 wk was required to significantly decrease trace metal concentrations in the upper mixed waters. The relatively slow rate of metal removal may be due, in part, to the low concentrations of particulate matter in the water column. Hem and coworkers (Smith 1971; Brown and Hem 1975) observed that rates of aluminum hydrolysis were very slow in synthetic solutions that did not contain particles. In the presence of elevated concentrations of mineral surfaces, however, solutions rapidly achieved equilibrium with respect to aluminum hydroxide solubility. In acidic lakes, conditions of disequilibrium with respect to aluminum hydroxide solubility have been noted. Schafran and Driscoll (1987) found that following internal ANC generation due to nitrate reduction, the water column of Dart's Lake became oversaturated with respect to aluminum hydroxide solubility and this condition persisted for extended periods of time. The long periods of oversaturation were attributed to low concentrations of suspended solids and a lack of nucleation sites to catalyze precipitation reactions.

It is unclear if the persistence of trace metals in the water column for several weeks after calcite addition had adverse effects on aquatic organisms. Immediately following base treatment, marked declines in populations of phytoplankton (Bukaveckas 1989) and zooplankton (Schaffner 1989) were evident in Woods Lake and Cranberry Pond, as have been reported in other studies (Scheider et al. 1975; Hultberg and Andersson 1982). This decline may have been due to direct mortality associated with changes in water chemistry or for phytoplankton, carbon growth limitations due to low concentrations of $CO_2$ (Bukaveckas 1989). It is also reasonable to suggest that the reduction in plankton immediately following base application may be due to coagulation with metal hydrolysis products and sedimentation from the water column (Baker et al. 1984). If so, the duration of plankton decline may be linked to the persistence of hydrolyzing metals (probably largely aluminum) in the water column.

There is concern that the persistence of high concentrations of trace metals following base treatment might restrict the success of fish restocking programs. However, Gloss et al. (1987) examined the mortality of brook trout (*Salvelinus fontinalis*) in cage trial experiments immediately after calcite treatment of Woods Lake and Cranberry Pond, and found good survival. It would appear that there is no cause for concern over metal toxicity to fish after base application to acidic lakes.

Base manipulation significantly altered trace metal transport in Wood Lake and Cranberry Pond. Rather than conservative transport or modest retention, these lakes became net sinks for trace metal inputs. While this manipulation results in an improvement of water quality (at least over the 3-mo duration of this study), it also coincides with enhanced deposition of trace metals to the sediments. A critical issue concerning the long-term success of base treatment programs is the ultimate fate of trace metals transported to lake sediments. If neutral conditions are maintained for an extended period, will the long-term accumulation of metals to sediments have deleterious effects on lake ecosystems? If a lake is treated for an extended period and then allowed to reacidify, will trace metals that have accumulated within sediments be remobilized to the water column at higher concentrations than previously existed? While these questions are critical to agencies considering base treatment as a management tool to renovate acidic lakes, information on the long-term consequences of metal retention is not currently available. Only through long-term study of chemically manipulated lake ecosystems will an understanding of the ultimate effects of base amendment be obtained.

## Acknowledgements

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# Chemical Response of Lakes Treated with $CaCO_3$ to Reacidification[1]

Charles T. Driscoll, William A. Ayling, G. F. Fordham, and Leah M. Oliver

*Department of Civil Engineering, Syracuse University, Syracuse, NY 13244, USA*

Driscoll, C. T., W. A. Ayling, G. F. Fordham, and L. M. Oliver. Chemical response of lakes treated with $CaCO_3$ to reacidification. Can. J. Fish. Aquat. Sci. 46: 258–267.

The reacidification of two lakes in the Adirondack region of New York treated by $CaCO_3$ application was evaluated. Base treatment resulted in a very high immediate dissolution efficiency in both lakes (78–82%), increasing acid neutralizing capacity (ANC) to values of 450 – 550 $\mu eq \cdot L^{-1}$. During the fall following manipulation, completely mixed water columns and elevated hydrologic inputs greatly facilitated reacidification, decreasing pH and diluting $Ca^{2+}$ concentrations. Cranberry Pond effectively reacidified within 7 mo of treatment, while the ANC of Woods Lake decreased to near 0 $\mu eq \cdot L^{-1}$ 15 mo after application. In Cranberry Pond, pH values decreased below 5.5 resulting in transport of elevated concentrations of inorganic Al through the lake. Annual ANC budgets suggest that little $CaCO_3$ penetrated to the sediments, limiting long-term release of ANC from sediment dissolution. Hydrolysis of Al, due to the elevated lake pH, served to consume ANC and there is evidence to indicate limited exchange of water column $Ca^{2+}$ with sediments shortly after treatment followed by release of this $Ca^{2+}$ during reacidification. However these processes did not significantly accelerate or attenuate the rate of reacidification. The rate of acidification could largely be explained by the flushing of ANC from the lakes by hydrologic inputs.

On a étudié la réacidification de deux lacs de la région des Adirondacks, (État de New York) traités au $CaCO_3$. Après l'application de cette base, le pouvoir de dissolution immédiate était très élevé dans les deux lacs (78–82 %), si bien que la capacité de neutralisation de l'acide (CNA) a atteint des valeurs se situant entre 450 et 550 $\mu eq \cdot L^{-1}$. L'automne suivant le traitement, étant donné que le mélange était complet dans la colonne d'eau et que l'apport hydrologique était important, la réacidification s'est trouvée considérablement accélérée, si bien que le pH et les concentrations de $Ca^{2+}$ ont baissé. À toutes fins utiles, l'étang Cranberry était réacidifié 7 mo après le traitement, tandis que la CNA du lac Woods était presque à 0 $\mu eq \cdot L^{-1}$ 15 mo après l'application de la base. Dans l'étang Cranberry, le pH a baissé sous 5,5, de sorte qu'il s'est transporté plus d'Al inorganique dans la nappe d'eau. D'après l'analyse des bilans annuels des substances à CNA, il s'est rendu peu de $CaCO_3$ jusqu'aux sédiments, ce qui limite la libération à long terme des substances à CNA par dissolution de sédiments. À cause de l'hydrolyse de l'Al qu'a entraînée l'augmentation du pH des eaux du lac, la CNa a baissé; d'après certaines observations, il y aurait eu des échanges limités entre le $Ca^{2+}$ de la colonne d'eau et les sédiments peu après le traitement, ce $Ca^{2+}$ étant ensuite libéré durant la réacidification. Néanmoins ces processus n'ont ni accéléré ni ralenti la réacidification dans une mesure significative. En grande partie, on peut expliquer la vitesse de l'acidification par l'effet de chasse qu'ont subi les substances à CNA à cause des apports hydrologiques.

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The effects of atmospheric deposition on the acidification of surface waters are well documented in the northeastern United States. (Driscoll and Newton 1985; Linthurst et al. 1986), southeastern Canada (Beamish and Harvey 1972; Jefferies et al. 1986), and Scandinavia (Henriksen 1979). In regions which exhibit limited release of basic cations ($Ca^{2+}$, $Mg^{2+}$, $Na^+$, $K^+$) from soil minerals, inputs of acidic deposition may not be completely neutralized resulting in pH values below 5.5 and elevated concentrations of Al in drainage waters. There is considerable concern over the impact of acidification on aquatic ecosystems, including increased bioavailability of trace metals (Baker 1982), effects on nutrient cycling (Dickson 1978), increased lake transparency causing a reduction in thermal stratification (Schofield 1972; Yan 1983), as well as effects on biological communities (Hall et al. 1980; Schofield and Driscoll 1987).

One approach that has been used to mitigate the effects of surface water acidification is treatment by base addition. Efforts to renovate the water chemistry and biology of acidic lakes by direct base application have generally been successful (e.g. Hultberg and Anderson 1982; Wright 1985). Base treatment results in increased pH and ANC, reduced trace metal concentrations, and increased diversity of aquatic organisms (Hultberg and Anderson 1982). However inputs of acidic water from precipitation, stream inflow, and groundwater cause reacidification and an eventual deterioration in water quality. Therefore, the rate of reacidification is an important economic and ecological consideration of base application strategies, because it regulates the duration and effectiveness of the treatment.

A number of studies (Dillon and Scheider 1984; Wright 1985) have investigated the reacidification of lakes treated by base addition and found that simple dilution of added base occurring

[1]This is part of a series of 13 papers devoted to the Lake Acidification Mitigation Project.

TABLE 1. Water chemical characteristics of study lake outlets prior to base treatment (mean ± standard deviation; $n = 23$).

| | Woods Lake | Cranberry Pond |
|---|---|---|
| pH | 4.8 ± 0.3 | 4.6 ± 0.2 |
| ANC ($\mu eq \cdot L^{-1}$) | −8 ± 14 | −14 ± 12 |
| $Ca^{2+}$ ($\mu eq \cdot L^{-1}$) | 68 ± 7 | 65 ± 4 |
| $Mg^{2+}$ ($\mu eq \cdot L^{-1}$) | 17 ± 2 | 18 ± 3 |
| $Na^{+}$ ($\mu eq \cdot L^{-1}$) | 21 ± 2 | 18 ± 3 |
| $K^{+}$ ($\mu eq \cdot L^{-1}$) | 7 ± 2 | 11 ± 3 |
| $SO_4^{2-}$ ($\mu eq \cdot L^{-1}$) | 119 ± 6 | 117 ± 4 |
| $NO_3^{-}$ ($\mu eq \cdot L^{-1}$) | 26 ± 17 | 42 ± 29 |
| $Cl^{-}$ ($\mu eq \cdot L^{-1}$) | 6 ± 2 | 6 ± 2 |
| DOC ($\mu mol\ C \cdot L^{-1}$) | 220 ± 59 | 350 ± 93 |
| DIC ($\mu mol\ C \cdot L^{-1}$) | 59 ± 32 | 74 ± 41 |
| Total Al ($\mu mol \cdot L^{-1}$) | 11.1 ± 6.5 | 17.3 ± 8.3 |
| Monomeric Al ($\mu mol \cdot L^{-1}$) | 7.5 ± 5.1 | 12.5 ± 7.5 |
| Nonlabile monomeric Al ($\mu mol \cdot L^{-1}$) | 1.3 ± 1.1 | 2.2 ± 1.7 |

by hydrologic inputs is generally inadequate to explain the rate of reacidification. The long-term release of $Ca^{2+}$ from $CaCO_3$ that settles to lake sediments following treatment often appears to be an important process retarding the rate of reacidification (Sverdrup and Bjerle 1983; Dillon and Scheider 1984; Wright 1985).

To answer critical questions concerning the ecological effects of liming, the multidisciplinary Lake Acidification Mitigation Project (LAMP) was initiated (Porcella 1989). The objective of the water chemistry component of LAMP was to evaluate the longer-term chemical response of chronically acidic lakes in the Adirondack region of New York to $CaCO_3$ treatment. We evaluated changes in water chemistry of two lakes for up to 15 mo following application of base. Specifically, we were interested in quantifying the changes in acid/base chemistry due to base application and evaluating the processes regulating the reacidification of these waters.

## Methods

The study lakes, Woods Lake (43°52′N, 71°58′W) and Cranberry Pond (43°51′N, 74°58′W), were chronically acidic prior to treatment (Schofield et al. 1985). Woods Lake and Cranberry Pond are shallow with extremely short, mean hydraulic residence times, 174 d and 63 d, respectively. (See Staubitz and Zarriello 1989).

Treatment of Woods Lake and Cranberry Pond occurred on 30 and 31 May 1985 with slurry additions of 22.6 and 7.2 t (dry basis), respectively, of finely powdered, high purity $CaCO_3$ (Porcella 1989).

Samples were collected for water chemistry analyses at the inlets, outlets, and at several depths (0,1,2,4,6,8,10, and 11 m in Woods Lake; 0,2,4, and 6 m in Cranberry Pond) from deep water column stations. Stations were sampled at approximately 3-wk intervals, with weekly sampling at the inlets and outlets during spring snowmelt. Water column samples were collected with a 4-L capacity Kemmerer sampler. A summary of the sampling and analytical program for the water chemistry component of the LAMP is available in Fordham and Driscoll (1989).

An evaluation of Al chemistry after base application was an important component of this study. To facilitate this analysis, the fractionation procedure of Driscoll (1984) was used. In this method, Al is partitioned into three fractions: labile monomeric Al, which is thought to represent inorganic complexes of aqueous Al; nonlabile monomeric Al, which is an estimate of

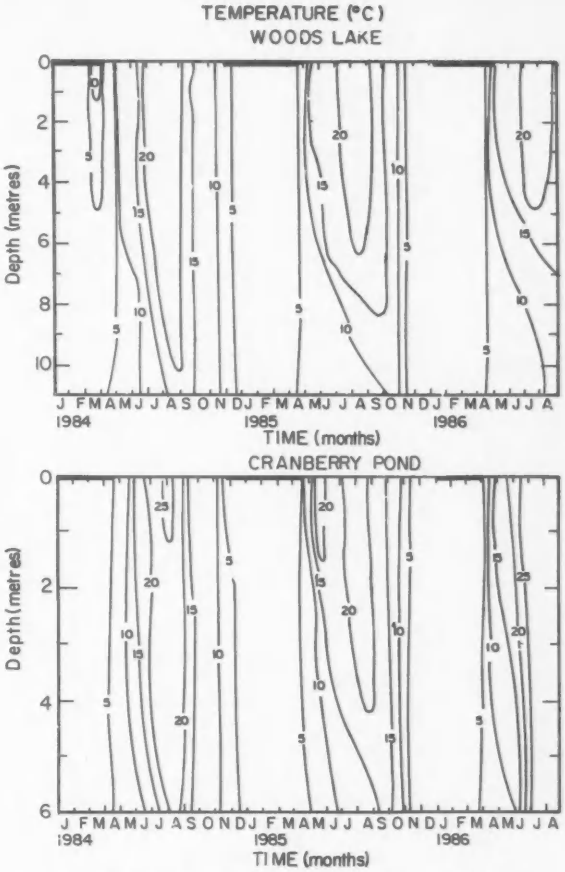



FIG. 1. Temperature isopleth of (a) Woods Lake and (b) Cranberry Pond during the study period.

organically bound Al; and acid-soluble Al, which is that fraction which requires acid digestion for detection and is considered to be colloidal/particulate Al or occluded alumino-organic materials. Using the water chemistry data collected from the LAMP, the distribution of inorganic Al was calculated with the chemical equilibrium model ALCHEMI (Schecher and Driscoll 1987).

Element mass balances were also calculated for both study lakes from the periods prior to (January 1984 to May 1985) and following treatment (June 1985 to August 1986) using the approach described by Fordham and Driscoll (1989).

## Results

Prior to base addition, the chemical characteristics of Woods Lake and Cranberry Pond (Table 1) were typical of clearwater acidic lakes. In both lakes, $SO_4^{2-}$ was the dominant anion and the equivalence of strong acid anions ($SO_4^{2-}$, $NO_3^{-}$, $Cl^{-}$) generally exceeded the equivalence of basic cations ($Ca^{2+}$, $Mg^{2+}$, $Na^{+}$, $K^{+}$). Consequently, high concentrations of acidic cations ($H^{+}$, $Al^{n+}$), were evident. Both lakes and inlet streams contained relatively low concentrations of dissolved organic carbon (DOC). Moreover, Woods Lake and Cranberry Pond showed

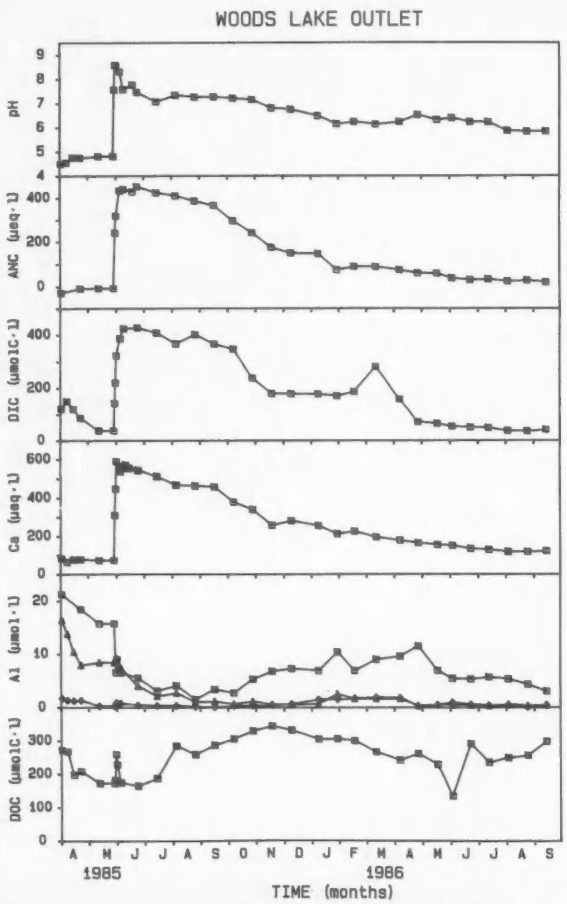



FIG. 2. Outlet chemistry of Woods Lake, including (a) pH, (b) acid neutralizing capacity (ANC), (c) $Ca^{2+}$, (d) dissolved inorganic carbon (DIC), (e) total, monomeric and nonlabile monomeric Al, and (f) dissolved organic carbon (DOC) following $CaCO_3$ treatment.

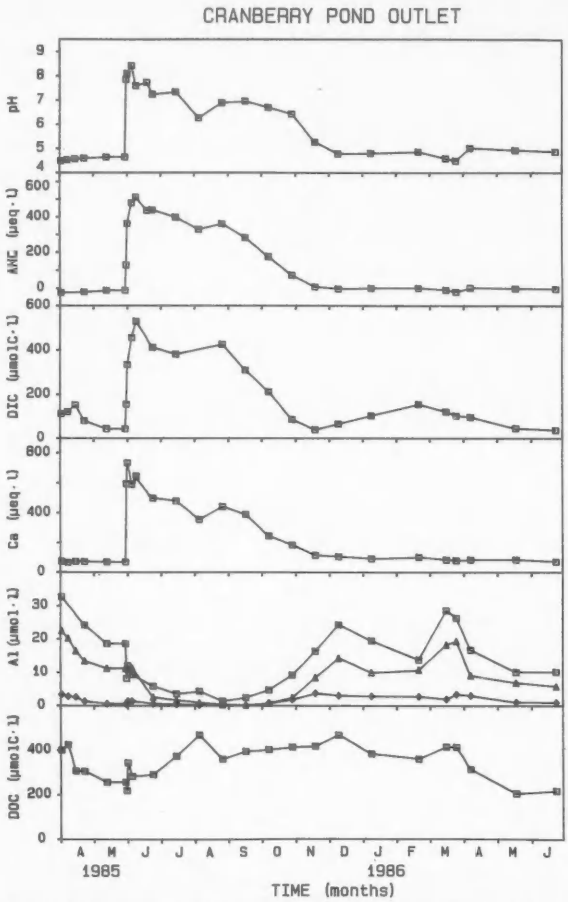



FIG. 3. Outlet chemistry of Cranberry Pond, including (a) pH, (b) acid neutralizing capacity (ANC), (c) $Ca^{2+}$, (d) dissolved inorganic carbon (DIC), (e) total, monomeric and nonlabile monomeric Al, and (f) dissolved organic carbon (DOC) following $CaCO_3$ treatment.

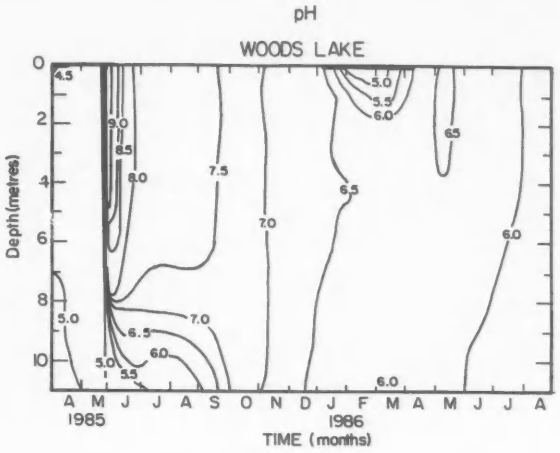
weak thermal stratification during the summer period prior to treatment (Fig. 1).

Dramatic changes in the water chemistry of Woods Lake and Cranberry Pond followed base application. Within hours after treatment, water column pH increased from below 5 to values above 9 (Fig. 2a, 3a, and 4). Large increases in acid neutralizing capacity (ANC; from below 0 to 200 $\mu eq \cdot L^{-1}$; Fig. 2b, 3b, and 5), $Ca^{2+}$ (from 50 to 300 $\mu eq \cdot L^{-1}$; Fig. 2d, 3d, and 6) and dissolved inorganic carbon (DIC) (from 35 to 150 $\mu mol\ C \cdot L^{-1}$; Fig. 1d, 2d, and 7) also occurred. ANC increases were essentially stoichiometric with increases in $Ca^{2+}$ (Fig. 8).

Due to preestablished thermoclines in both lakes, base treatment did not penetrate through the entire water column. In Woods Lake the thermocline was located at approximately 8 m (Fig. 1a). Apparently the particle size of $CaCO_3$ was so small (median diameter 2 μm) that little material migrated to the lower waters. Visual observation revealed an accumulation of $CaCO_3$ particles just above the thermocline. As a result of these conditions, changes in water quality were largely restricted to the epilimnion during the summer stratification period. Within the hypolimnion of Woods Lake (below 9 m), pH values remained below 6.5, ANC below 200 $\mu eq \cdot L^{-1}$ and $Ca^{2+}$ below 100 $\mu eq \cdot L^{-1}$ from the time of base addition (May 30) through much of summer stratification (until September 1985). A similar condition was also evident in Cranberry Pond, because of its shallower depth and weaker stratification (Fig. 1b), however, greater treatment of the lower waters occurred. A very low percentage (< 5%) of total lake volume was left untreated in Woods Lake and Cranberry Pond.

Within 2–4 wk following base application, pH values of both lakes decreased below 8 (Fig. 2a, 3a, and 4) while ANC (450–550 $\mu eq \cdot L^{-1}$; Fig. 5), $Ca^{2+}$ (500–600 $\mu eq \cdot L^{-1}$; Fig. 6) and DIC (400–450 $\mu mol\ C \cdot L^{-1}$; Fig. 7) reached maximum values in the upper mixed waters. A detailed description of acid/base chemistry immediately following base application is provided in Fordham and Driscoll (1989). After manipulation both lakes exhibited stronger thermal stratification (Fig. 1).

Concentrations and speciation of Al were significantly altered following base treatment. Labile (inorganic) monomeric Al decreased to concentrations below 2 $\mu mol \cdot L^{-1}$ within 4 wk after treatment in Cranberry Pond and 12 wk after treatment of Woods Lake (Fig. 9). No changes in nonlabile (organic) mon-



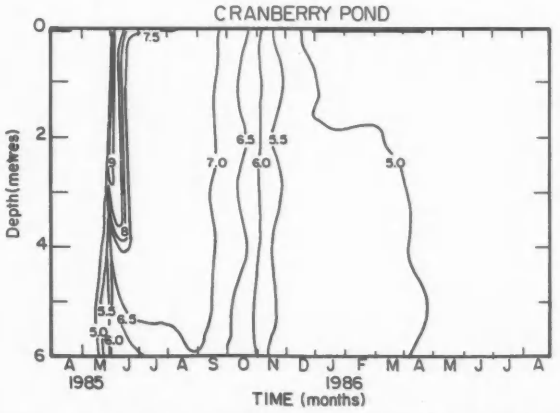
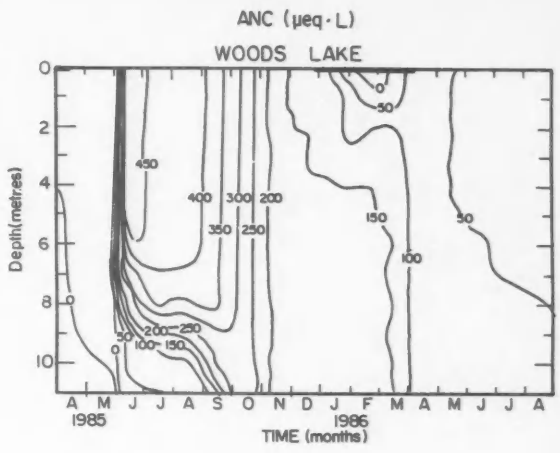




FIG. 4. pH isopleths of (a) Woods Lake and (b) Cranberry Pond from April 1985 to August 1986. Base treatment occurred on 30 and 31 May 1985.



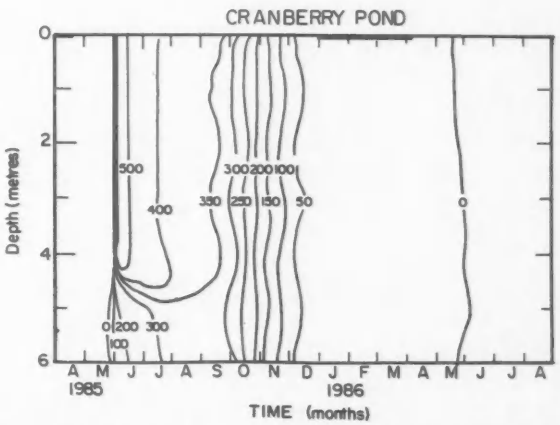




FIG. 5. Acid neutralizing capacity (ANC) of (a) Woods Lake and (b) Cranberry Pond from April 1985 to August 1986. Base treatment occurred on 30 and 31 May 1985.

omeric Al were evident following the manipulation (Fig. 2e, and 3e).

After the low flow period during summer 1985, pronounced decreases in pH (Fig. 2a, 3a, and 4), ANC (Fig. 2b, 3b, and 5), $Ca^{2+}$ (Fig. 2d, 3d, and 6), and DIC (Fig. 2c, 3c, and 7) were observed in both lakes associated with elevated discharge during the fall (Staubitz and Zarriello 1989). By the ice-cover period in December 1985, the ANC decreased below 200 $\mu eq \cdot L^{-1}$ (Figs. 2b, 5a) and $Ca^{2+}$ concentrations decreased below 300 $\mu eq \cdot L^{-1}$ (Fig. 2d, and 6a) in Woods Lake. pH values were near neutral (6.5–7.0; Fig. 4a) and concentrations of labile (inorganic) monomeric Al remained very low (< 1 $\mu mol \cdot L^{-1}$; Fig. 2e, and 9a). Cranberry Pond reacidified much faster than Woods Lake as its pH values decreased below 5.5, ANC decreased below 50 $\mu eq \cdot L^{-1}$ and $Ca^{2+}$ decreased below 150 $\mu eq \cdot L^{-1}$ by December 1985. In effect, Cranberry Pond completely reacidified within 7 mo following treatment. Marked increases in labile monomeric Al were evident in Cranberry Pond as pH values decreased below 5.5 (Fig. 3e, and 9b).

The ANC of Woods Lake remained between 100 and 200 $\mu eq \cdot L^{-1}$ in early winter. During this period, DIC values (Fig. 7a) increased in the lower waters due to microbial production of $CO_2$ and as a result pH values decreased (Fig. 4a). However, release of $Ca^{2+}$ to the lower waters from sediments was not evident (Fig. 6a). During the later stages of the ice-cover period, acidic water entered the lake from the surrounding watershed at 0°C and migrated along the ice/water interface to the outlet. A decrease in pH (Fig. 4a), ANC (Fig. 5a), and $Ca^{2+}$ (Fig. 6a), and an enrichment in labile (inorganic) monomeric Al concentrations (Fig. 9a) was evident during this period; however, the inverse thermal stratification restricted this reacidification to a depth of less than 2 m. Peak snowmelt discharge occurred during the last week of March and the first week of April (Staubitz and Zarriello 1989).

Immediately following ice-out, the ANC of Woods Lake was reduced below 100 $\mu eq \cdot L^{-1}$ while its pH remained above 6. During the low-flow summer period, reacidification proceeded slowly. In the epilimnion, pH and ANC reached minimum values of 5.8 and 23 $\mu eq \cdot L^{-1}$, respectively. In the hypolimnion, however, ANC values exceeded 100 $\mu eq \cdot L^{-1}$, largely due to microbial reduction reactions which resulted in $NH_4^+$ ($\Delta$18 $\mu eq \cdot L^{-1}$) and $Fe^{2+}$ ($\Delta$ 8 $\mu eq \cdot L^{-1}$) release as well as $NO_3^-$ ($\Delta$ 23 $\mu eq \cdot L^{-1}$) retention. Limited reduction of solutes

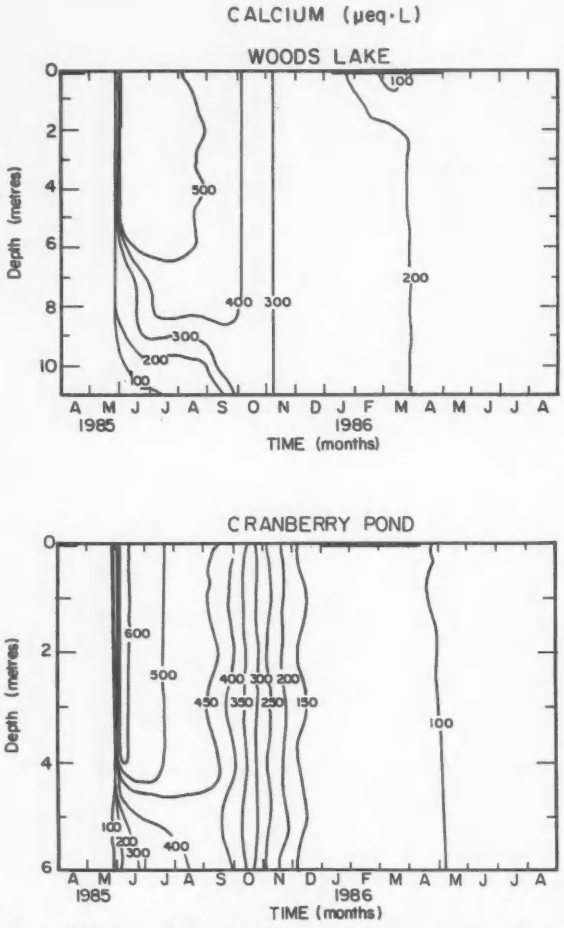



FIG. 6. Calcium isopleth of (a) Woods Lake and (b) Cranberry Pond from April 1985 to August 1986. Base treatment occurred on 30 and 31 May 1985.

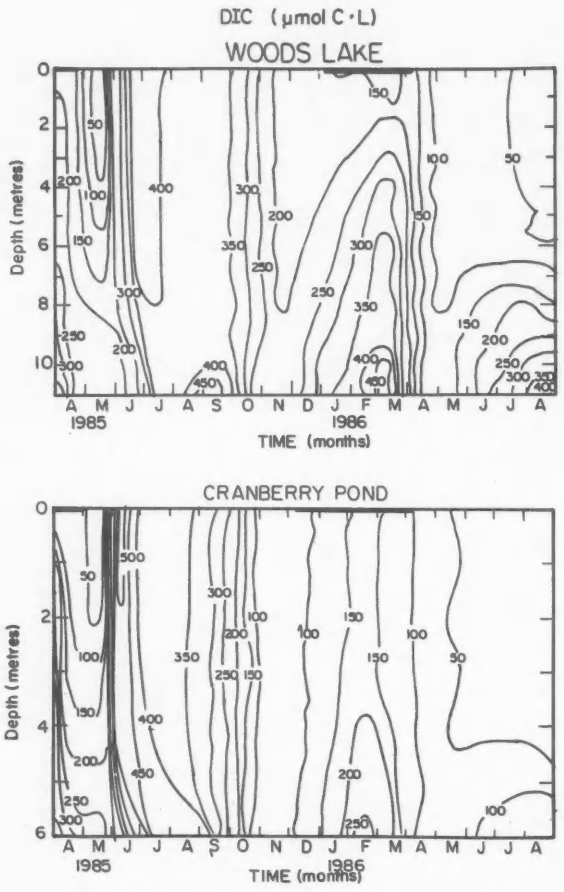



FIG. 7. Dissolved inorganic carbon (DIC) isopleth of (a) Woods Lake and (b) Cranberry Pond from April 1985 to August 1986. Base application occurred on 30 and 31 May 1985.

occurred despite water column $O_2$ concentrations above 50 $\mu mol \cdot L^{-1}$ (Fig. 10). Labile (inorganic) monomeric Al concentrations remained low in the water column because of low concentrations in the inlet streams and elevated pH values in the water column.

Intriging patterns in Al chemistry were evident during reacidification of these lakes. In the summer immediately following base application (1985), concentrations of all fractions of Al were low. During the fall increased concentrations of labile (inorganic) monomeric Al in inlet streams resulted in higher water column concentrations. In circumneutral Woods Lake, increases in Al occurred as the acid-soluble form (Fig. 2e, and 11a). As Cranberry Pond rapidly reacidified (Fig. 4b), increased Al was evident as both labile (inorganic) monomeric (Fig. 3e, and 9b) and acid-soluble fractions (Fig. 3e, and 11b). The conversion of inputs of labile (inorganic monomeric) Al to acid-soluble Al was particularly evident during ice-cover and immediately following ice-breakup in Woods Lake. Elevated concentrations of labile (inorganic) monomeric Al originating from inlet waters were apparent along the ice/water interface during ice-cover (above 1–2 m). Immediately below this depth, high concentrations of acid-soluble Al were observed. Moreover, following ice break-up when Woods Lake was completely mixed, high concentrations of acid-soluble Al were evident throughout the water column. These patterns suggest that labile (inorganic) monomeric Al was converted to acid soluble Al through hydrolysis reactions as acidic inputs mixed with neutral lake water.

Shifts in the speciation of Al were also apparent from mass–balance calculations (Table 2). Prior to and following treatment, some retention of nonlabile (organic) monomeric Al (15.5 $mmol \cdot m^{-2} \cdot yr^{-1}$), labile (inorganic) monomeric Al (26.5 $mmol \cdot m^{-2} \cdot yr^{-1}$), and acid soluble Al (3.3 $mmol \cdot m^{-2} \cdot yr^{-1}$) was evident in Woods Lake. In Cranberry Pond, retention of nonlabile (organic) monomeric Al (27.9 $mmol \cdot m^{-2} \cdot yr^{-1}$) and labile (inorganic) monomeric Al (22.1 $mmol \cdot m^{-2} \cdot yr^{-1}$) occurred, along with a small release of acid soluble Al (4.4 $mmol \cdot m^{-2} \cdot yr^{-1}$). Although there was some retention of Al in these systems, most of Al inputs were transported out the lake outlet and labile (inorganic) monomeric Al was the major form of Al in outlet waters (Table 2).

Dramatic changes in the transport of Al occurred after base treatment (Table 2). In circumneutral Woods Lake, inputs of

TABLE 2. Comparison of the transport (in $mmol \cdot m^{-2} \cdot yr^{-1}$) and distribution of Al in inlet and outlet waters, and lake retention, prior to (June 1984 – May 1985) and following (June 1985 – May 1986) base application to Woods Lake and Cranberry Pond.

| | Woods Lake | | | | | Cranberry Pond | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | *Pretreatment* | | | | | |
| Al fractions | Stream influx | % | Lake efflux | % | Lake retention | Stream influx | % | Lake efflux | % | Lake retention |
| Nonlabile (organic monomeric | 20.1 | 17.3 | 8.0 | 12.2 | 15.5 | 52.7 | 17.8 | 31.2 | 12.5 | 27.9 |
| Labile (inorganic) monomeric | 68.4 | 59.0 | 42.7 | 65.3 | 26.5 | 187.6 | 63.5 | 160.9 | 64.9 | 22.1 |
| Acid-soluble | 27.4 | 23.7 | 14.7 | 22.5 | 3.3 | 55.2 | 18.7 | 56.8 | 22.8 | −4.4 |
| Total | 115.9 | 100 | 65.4 | 100 | | 295.5 | 100 | 248.9 | 100 | |
| | | | | | *Posttreatment* | | | | | |
| Nonlabile (organic) monomeric | 19.8 | 16.3 | 6.4 | 12.3 | 12.2 | 52.3 | 18.9 | 34.0 | 17.1 | 17.7 |
| Labile (inorganic) monomeric | 58.6 | 48.0 | 3.3 | 6.4 | 81.0 | 145.4 | 52.7 | 75.7 | 38.2 | 85.4 |
| Acid-soluble | 43.6 | 35.7 | 42.3 | 81.3 | 2.4 | 78.3 | 28.4 | 88.7 | 44.7 | −2.2 |
| Total | 122.0 | 100 | 52.0 | 100 | | 276.0 | 100 | 198.4 | 100 | |

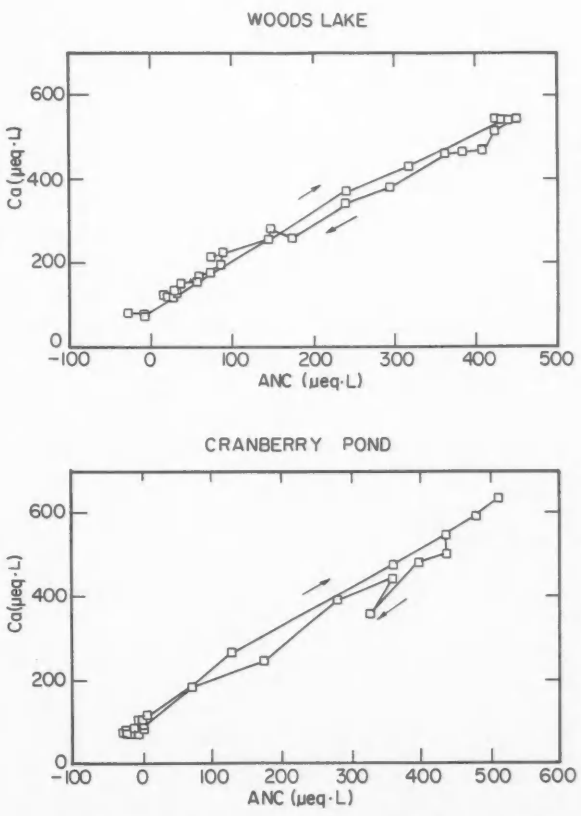



FIG. 8. Outlet concentrations of $Ca^{2+}$ as a function of acid neutralizing capacity (ANC) of (a) Woods Lake and (b) Cranberry Pond over the manipulation and reacidification periods.

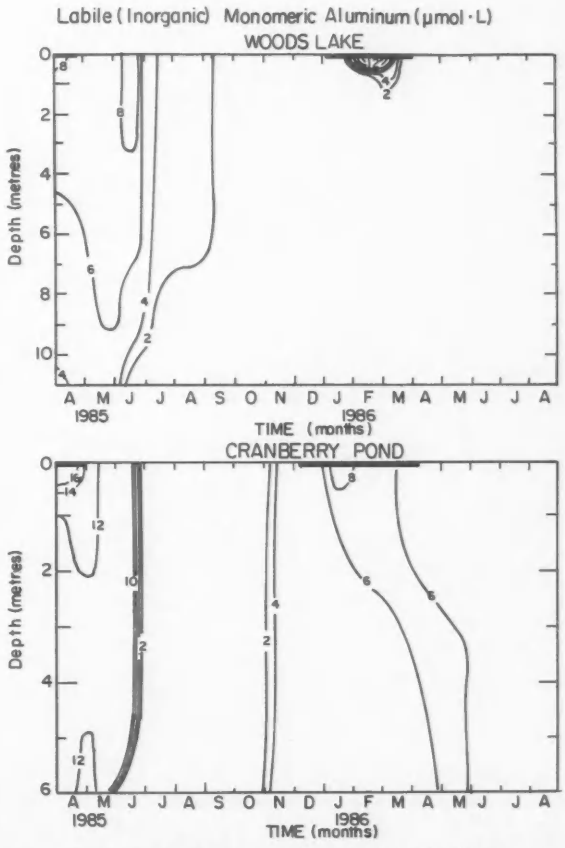



FIG. 9. Labile (inorganic) monomeric Al isopleth of (a) Woods Lake and (b) Cranberry Pond from April 1985 to August 1986. Base addition occurred on 30 and 31 May 1985.

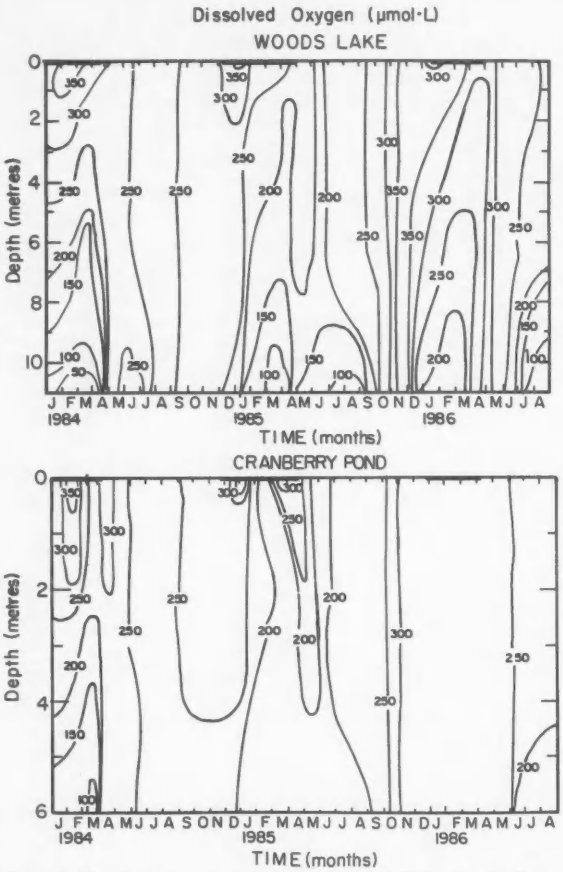



FIG. 10. Dissolved oxygen isopleth of (a) Woods Lake and (b) Cranberry Pond during the study period.

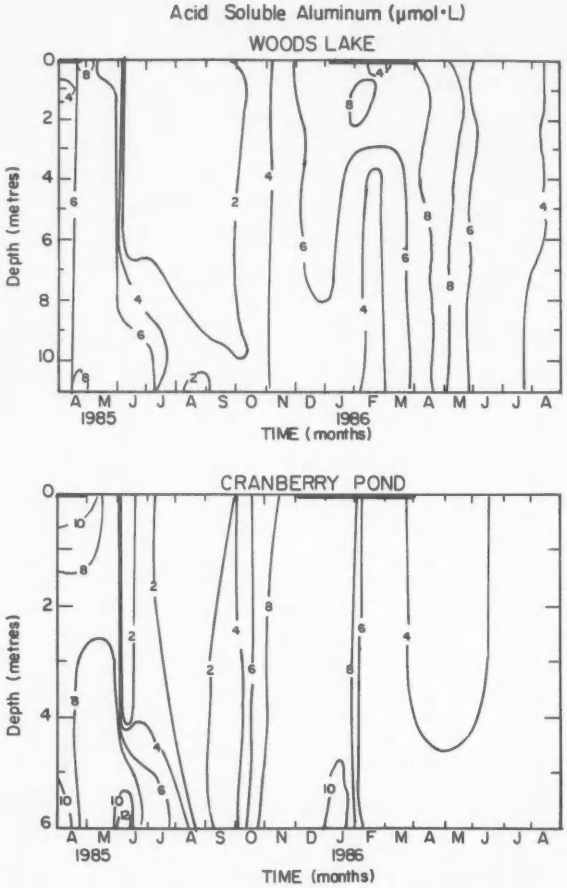
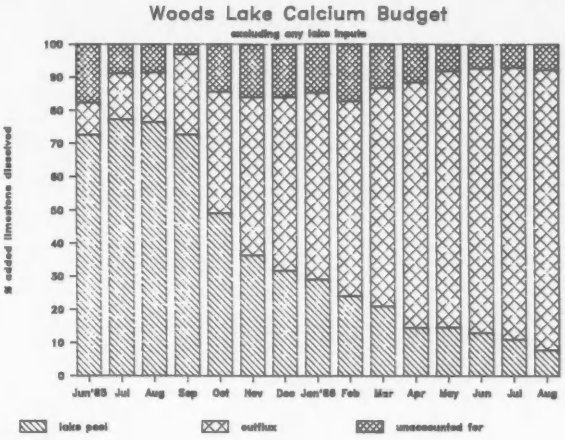
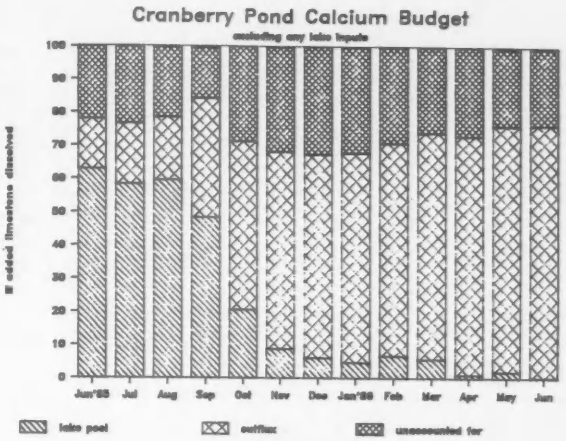


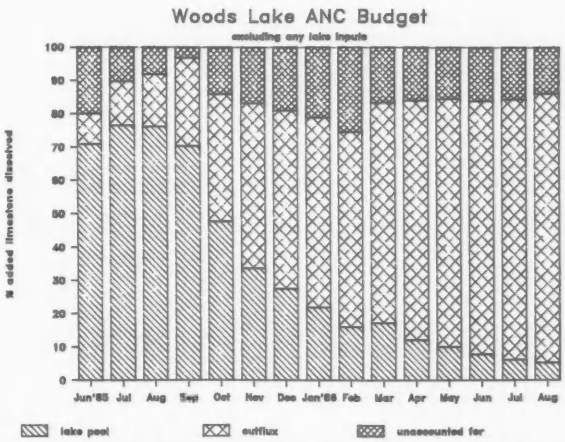

FIG. 11. Acid soluble Al isopleth of (a) Woods Lake and (b) Cranberry Pond from April 1985 to August 1986. Base addition occurred on 30 and 31 May 1985.

labile (inorganic) monomeric Al were almost completely retained (81.0 mmol·m$^{-2}$·yr$^{-1}$) with limited export occurring only during ice-cover with snowmelt (Fig. 9a). Although Cranberry Pond reacidified within a few months after treatment, considerable retention of labile (inorganic) monomeric Al was also evident (85.4 mmol·m$^{-2}$·yr$^{-1}$). In both systems retention of nonlabile (organic) monomeric Al occurred (12.2 and 17.7 mmol·m$^{-2}$·yr$^{-1}$ for Woods Lake and Cranberry Pond, respectively). Although these values are reduced from pretreatment conditions, it is not clear that base application affected this process. In both Woods Lake and Cranberry Pond, inputs of acid-soluble Al closely balanced outputs (2.4 mmol·m$^{-2}$·yr$^{-1}$ retention and 2.2 mmol·m$^{-2}$·yr$^{-1}$ release, respectively). From water column observations (Fig. 9, and 11) it is doubtful that the acid-soluble Al fraction was conservative within these lakes. Rather, export of this Al form was undoubtedly due to a combination of lake inputs as well as in-lake hydrolysis from monomeric forms.

Mass balance calculations on Ca and ANC for both lakes indicate the rate and extent of reacidification. The initial dissolution efficiency (1 mo after treatment) of added $CaCO_3$ based on measured Ca was very high in both lakes, 82% for Woods Lake and 78% for Cranberry Pond (Fig. 12, and 13). The unaccounted Ca in mass balances was evidently deposited to sediments as particulate $CaCO_3$ or exchanged on sediment functional groups (Young et al. 1989). After treatment, added Ca and ANC were largely flushed from the lakes. The rates of Ca and ANC loss were most pronounced during the fall following application. This period coincided with completely mixed or almost completely mixed water columns and elevated inflows associated with large hydrologic events (Staubitz and Zarriello 1989), which greatly facilitated reacidification. By November 1985 only 36% of the added Ca and 35% of the added ANC were evident in Woods Lake. In Cranberry Pond only 9% of the added Ca and 6% of the added ANC were remaining by November 1985, indicating that reacidification was essentially complete. After ice-cover, reacidification proceeded slower in Woods Lake. Although elevated discharge was evident in March/April 1986 (Staubitz and Zarriello 1989), inverse thermal stratification during ice-cover restricted the mixing of inlet water with bulk lake water thereby limiting the export of Ca and ANC. By the end of the monitoring period (August 1986), only 8% of the added Ca and 5% of the added ANC remained in Woods Lake. The dissolution efficiency calculated from Ca mass balances increased slightly to 92% suggesting that limited release of Ca from sediments through $CaCO_3$ dissolution or cation exchange had occurred. In Cranberry Pond the moni-



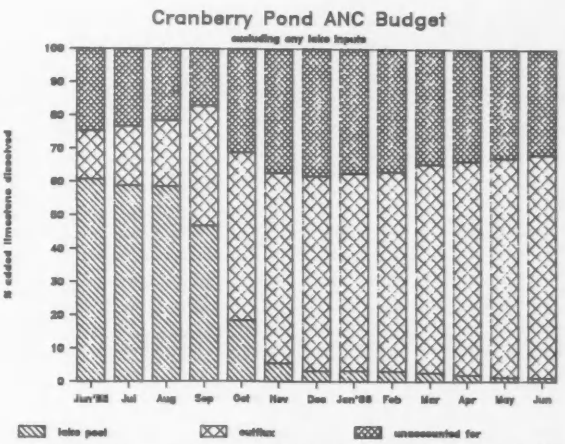




FIG. 12. Relative cumulative monthly budgets of (a) Ca and (b) acid neutralizing capacity (ANC) for Woods Lake following $CaCO_3$ treatment. The fluxes include lake pools, stream efflux, and any net loss due to discrepancies in mass balances. Inputs were subtracted from the budgets.

FIG. 13. Relative cumulative monthly budget of (a) $Ca^{2+}$ and (b) acid neutralizing capacity (ANC) for Cranberry Pond following $CaCO_3$ treatment. Fluxes include lake pool, stream efflux, and any net loss due to discrepancies in mass balances. Inputs were subtracted from the budgets.

toring program was terminated in June 1986; by this period 0% of the added Ca and 1% of the added ANC remained in the water column. Moreover, a final dissolution efficiency of 77% was calculated from Ca mass balances. This value is very similar to the initial dissolution efficiency suggesting that little additional release of Ca and ANC occurred from the sediments of Cranberry Pond during the 13 mo following treatment.

Changes in lake chemical processes due to base addition may mitigate or accelerate reacidification. Most lakes naturally produce ANC through the retention of $SO_4^{2-}$ and $NO_3^-$ (Kelly et al. 1982). While the extent of these processes varies widely (Kelly et al. 1987), they can be an important source of ANC. Because base addition tends to increase productivity (Dillon et al. 1979), strengthen the thermal structure of lakes, and lengthen the stratification period (Yan 1983), it is reasonable to hypothesize that the importance of microbial reduction processes may increase in treated systems. Increased in-lake retention of $NO_3^-$ and $SO_4^{2-}$ may serve to retard reacidification. Woods Lake and Cranberry Pond were good candidates to test this hypothesis because they were weakly stratified prior to base application and more strongly stratified following treatment (Fig. 1). Mass balance calculations revealed that Woods Lake generated a net ANC of 88 $meq \cdot m^{-2} \cdot yr^{-1}$ and Cranberry Pond produced a net ANC of 214 $meq \cdot m^{-2} \cdot yr^{-1}$ for the pretreatment period June 1984 to May 1985. In both lakes a net release of basic cations as well as microbial reduction reactions were largely responsible for the production of ANC. This generation of ANC was offset by in-lake processes producing acidity, principally the hydrolysis of Al (Table 2). In-lake processes did not significantly increase the ANC of either Woods Lake or Cranberry Pond, as the net, flow-weighted increase in ANC between inlet and outlet waters were only 1.2 and 7.0 $\mu eq \cdot L^{-1}$, respectively.

A change in the acid/base chemistry of Woods Lake and Cranberry Pond was evident after base application. Most apparent was that these lakes shifted from net sources to net sinks of ANC (Fig. 14). While processes contributing to the generation of ANC increased slightly for Woods Lake (154 pretreatment to 235 posttreatment $meq \cdot m^{-2} \cdot yr^{-1}$) and Cranberry Pond (216 pretreatment to 269 posttreatment $meq \cdot m^{-2} \cdot yr^{-1}$) following the manipulation, these increases were relatively small and may be

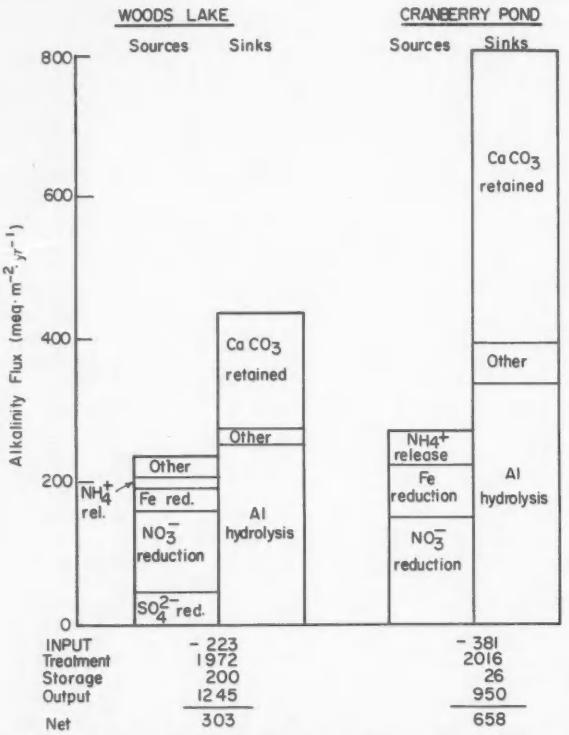



FIG. 14. Acid neutralizing capacity (ANC) budgets for Woods Lake and Cranberry Pond for the 12-mo period immediately following base treatment. Contributions to the ANC budgets were determined from mass balances on individual ions. Measured ANC balances are indicated.

due to year-to-year differences in lake processes rather than the effects of base application. Moreover, no significant change in water column oxygen concentrations were evident (Fig. 10). However, in-lake processes that consume ANC increased following base treatment. In particular Al hydrolysis caused a large increase in ANC consumption (80 pretreatment to 243 posttreatment, in meq·m$^{-2}$·yr$^{-1}$ for Woods Lake and 66 pretreatment to 332 posttreatment, in meq·m$^{-2}$·yr$^{-1}$ for Cranberry Pond; Fig. 13). Calcium retained within the lakes, based on Ca mass balances, also represented an important sink of ANC of both lakes for the year after base application (Fig. 14). The net loss of ANC, based on ANC mass balances, were generally consistent with values calculated from individual element budgets (303 measured versus 200 from element balances, in meq·m$^{-2}$·yr$^{-1}$ for Woods Lake; 658 measured versus 533 from element balances, in meq·m$^{-2}$·yr$^{-1}$ for Cranberry Pond; Fig. 14). These discrepancies could be explained by a combination of analytical error, unmeasured chemical parameters (such as organic acids), uncertainity in hydrology, uncertainity in lake pools, or uncertainity in the chemical concentrations of inflows and outflows. Given the short hydraulic retention times of these lakes, the agreement between measured ANC and calculated values based on element budgets is reasonable.

## Discussion

The reacidification of Woods Lake and Cranberry Pond, shortly after base application, may be attributed to the short hydraulic retention times of both systems (174 d for Woods Lake and 63 d for Cranberry Pond; Staubitz and Zarriello 1989). While these values are indeed short, they are not atypical for the Adirondack region. From the United States Environmental Protection Agency, Eastern Lake Survey, the mean retention time for Adirondack Lakes with surface areas between 4 and 2000 ha is 0.62 ± 1.27 yr ($n$ = 180; Linthurst et al. 1986). Based on this survey, Woods Lake and Cranberry Pond are in the 80 and 59 percentile, respectively.

Unlike other studies (Sverdrup and Bjerle 1983; Dillon and Scheider 1984; Wright 1985), the reacidification rate of Woods Lake and Cranberry Pond can largely be explained by dilution of the $CaCO_3$ treatment from hydrologic inputs. Our ANC budgets show that for the period following base application, ANC added from $CaCO_3$ was largely exported through the lake outlets (63 and 47% of treatment ANC for Woods Lake and Cranberry Pond, respectively). The remaining ANC was either neutralized by strong acid inputs, remained as lake storage, or was unaccounted in mass balances (Fig. 12, 13, and 14). Net loss (discrepancy) in added ANC that occurred in Woods Lake (303 meq·m$^{-2}$·yr$^{-1}$) and Cranberry Pond 658 meq·m$^{-2}$·yr$^{-1}$) could largely be explained by unrecovered Ca associated with the $CaCO_3$ treatment (160 and 480 meq·m$^{-2}$·yr$^{-1}$, respectively). If unrecovered Ca is not considered in ANC budgets, a net consumption of ANC is still evident in both lakes following treatment (Fig. 14). The fact that treated lakes acted as a net sink of ANC is largely due to the increased hydrolysis of Al associated with the neutral pH values. It appears that when acidic systems with short hydraulic residence times are treated by base application, increased consumption of ANC due to Al hydrolysis is quantitatively more important than any increased production of ANC due to stimulation of microbial reduction. Although the study lakes shifted from net production to net consumption of ANC due to base treatment, the magnitude of these changes appeared to have a negligible effect on the rate of reacidification.

Other researchers have reported that long-term release of Ca from sediments is an important process retarding reacidification of treated lakes (Sverdrup and Bjerle 1983; Dillon and Scheider 1984; Wright 1985). While this process undoubtedly occurred in Woods Lake and Cranberry Pond, it was quantitatively unimportant in the treatments studied here. The very small particle sizes (median diameter 2 μm) of the added $CaCO_3$ coupled with preestablished thermal stratification restricted settling and greatly enhanced the initial dissolution efficiency (Fordham and Driscoll 1989). Values of initial dissolution efficiency reported for Woods Lake and Cranberry Pond were considerably higher than the range of 17 – 42% reported by Sverdrup and Bjerle (1983) for nine $CaCO_3$-treated lakes in Sweden and Norway. The relatively complete initial dissolution suggests that a small percentage of the added Ca was deposited to the sediments (Young et al. 1989), as such only a small pool of sediment Ca was available for long-term release in these lakes. Additional release of Ca after the first month following treatment was evident only in Woods Lake (Fig. 11), and this long-term release represented a small fraction of the total Ca budget (10%). Indeed mass balances suggest that much of this "long-term" release of Ca from Woods Lake occurred during the summer stratification period immediately following base application. Close examination of water column profiles for both lakes during winter ice-cover (1986) and summer stratification show no evidence of increased $Ca^{2+}$ concentrations near the sediment/water interface. If sediment release of Ca was an important process, pat-

terns of $Ca^{2+}$ diffusion from the lower water should be evident (Fig. 6), particularly during the ice-cover period when elevated $CO_2$ facilitates $CaCO_3$ dissolution (DePinto et al. 1989).

As part of the LAMP study, model simulations by DePinto et al. (1989) suggested that sediments retain $Ca^{2+}$ through cation exchange reactions immediately following base application and subsequently release it during reacidification. There is limited evidence to demonstrate the occurrence of this process in Woods Lake and Cranberry Pond through outlet concentrations of $Ca^{2+}$ as a function of ANC (Fig. 8). The outlet response of both lakes were close to stoichiometric, with a 1:1 increase in $Ca^{2+}$ and ANC following application and decrease during reacidification. However, close examination of these plots reveals a slight hystersis. During the initial stages of reacidification of Woods Lake and Cranberry Pond, outlet concentrations of $Ca^{2+}$ were slightly lower ($10-25\ \mu eq \cdot L^{-1}$) for a given value of ANC than observed during stoichiometric increase, suggesting a slight retention of $Ca^{2+}$ immediately after treatment. This relative depletion of $Ca^{2+}$ was evident during much of the reacidification period. However, as ANC decreased below $150\ \mu eq \cdot L^{-1}$ for Woods Lake and $80\ \mu eq \cdot L^{-1}$ for Cranberry Pond, $Ca^{2+}$ concentrations increased relative to ANC, actually exceeding the stoichiometry observed immediately following base treatment. These patterns are qualitatively consistent with the sediment exchange hypothesis of DePinto et al. (1989) and suggest that shortly after treatment, sediments retain water column $Ca^{2+}$ and as a lake reacidifies this $Ca^{2+}$ is released back to the water column. However, the magnitude of this retention/release of $Ca^{2+}$ was small and not quantitatively important in attenuating the rate of reacidification (DePinto et al. 1989).

## Conclusions

Results of this study have important implications concerning the treatment of acidic lakes. Logistically it would be difficult to implement regional base treatment programs in lake districts with characteristically short hydraulic residence times, like the Adirondacks. Treatment strategies promoting a relatively large initial dissolution of $CaCO_3$ are not appropriate for lakes with short flushing rates, as ANC is rapidly exported from the water column and treatment would have to be repeated at frequent intervals. An alternative strategy might be a lower initial dissolution efficiency coinciding with sediment $CaCO_3$ treatment. (Woods Lake was treated again in September 1986 using this approach). The long-term release of $Ca^{2+}$ from sediment dissolution may help delay reacidification; however this process may be difficult to predict quantitatively (Sverdrup and Bjerle 1983). In lakes with extremely short flushing rates, like Cranberry Pond, even sediment treatment may not be adequate to delay reacidification, greatly limiting the feasibility of direct lake treatment. Such systems may require alternative treatment approaches such as stream or watershed applications (e.g. Bengtsson et al. 1980).

## Acknowledgements

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# Hydrology of Two Headwater Lakes in the Adirondack Mountains of New York[1]

Ward W. Staubitz and Phillip J. Zarriello

*Water Resources Division, U.S. Geological Survey, 521 W. Seneca St., Ithaca, N.Y. 14850*

Staubitz, W. W., and P. J. Zarriello. 1989. Hydrology of two headwater lakes in the Adirondack mountains of New York. Can. J. Fish. Aquat. Sci. 46: 268–276.

Cranberry Pond and Woods Lake are small, acidic headwater lakes in the west-central Adirondack region of New York State. The lakes differ in size and depth but have similar watershed characteristics. Both watersheds contain thin eolian and sandy till deposits overlying granitic gneiss and have limited capacity to store and transmit groundwater. Total lake inflow was calculated as a residual of a monthly hydrologic balance based on measured precipitation, lake outflow, change in lake storage, and estimated evaporation; surface-water and groundwater inflow to each lake also were estimated. Results indicate that the lakes are hydrologically similar and are dominated by surface-water systems with highly variable runoff that responds rapidly to precipitation. Groundwater, which constituted about 16% of the total inflow to Cranberry Pond and from 31 to 38% of the total inflow to Woods Lake in 1984–86, moves through a shallow flow system that provides little stabilizing influence on the hydrology or water chemistry of the lakes. Error analysis of the hydrologic balance indicated that total annual inflow, calculated as a residual of the hydrologic balance, is accurate to within 12%. Calculated monthly inflow values are subject to greater potential error that ranges up to 46%.

L'étang Cranberry et le lac Woods sont deux petits lacs de tête aux eaux acidifiées; ils se trouvent dans le centre-ouest des Adirondacks, dans l'État de New York. Leur étendue et leur profondeur sont différentes, mais les caractéristiques de leur bassin versant sont semblables. Ainsi, les deux bassins versants comportent de minces dépôts éoliens et du till sableux superposés à du gneiss granitique et sont limités quant à leur capacité d'emmagasinement et de transmissivité aquifères. On a calculé le débit entrant total en faisant le bilan hydrologique mensuel d'après les précipitations mesurées, le débit sortant, la variation de l'emmagasinement et l'évaporation estimée; on a aussi fait l'estimation du débit entrant des eaux de surface et des eaux souterraines dans chacun des lacs. D'après les résultats, les lacs sont hydrologiquement semblables et leur alimentation dépend surtout de systèmes de surface où le ruissellement, très variable, change rapidement en fonction des précipitations. Les eaux souterraines, qui représentaient environ 16 % du débit entrant total dans l'étang Cranberry et de 31 à 38 % dans le lac Woods en 1984–86, s'écoulent dans un système peu profond sans grande influence stabilisatrice sur l'hydrologie des lacs ou sur la chimie des eaux. D'après l'analyse de l'erreur du bilan hydrologique, le débit entrant total annuel, calculé d'après le bilan hydrologique, est exact à 12 % près. Avec le calcul du débit entrant mensuel, l'erreur peut être de 46 %, ce qui est plus élevé.

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The occurrence of acidic deposition in the eastern United States, Canada, and Europe has been well documented (Likens 1976; Peters and Bonelli 1982). Neutralization of acidic deposition within the watershed is a function of the mineral composition of bedrock and surficial deposits and the quantity and rate of groundwater flow through those materials (Peters and Murdoch 1985). The flow paths along which water moves enroute to a lake, the volume of surface-water inflows in relation to the volume of groundwater inflows, and the timing of precipitation can appreciably influence the amount of acid neutralization that occurs in each watershed (April and Newton 1985).

Alkaline materials can be added to lakes in watersheds that lack adequate neutralization capacity to increase the buffering capacity of the lake. In 1984, the Lake Acidification Mitigation Project (LAMP) began to study the physical, chemical, and biological response of lakes to base addition (Porcella 1989). As part of the study, the U.S. Geological Survey measured the hydrologic balance of two lakes to provide a measure of the spatial and temporal distribution of water entering and exiting the lakes. The hydrologic balance, coupled with water quality data collected by other investigators (Fordham and Driscoll 1989), provided data necessary for the calculation of the mass balance of acidity, acid-neutralizing capacity, and individual chemical constituents that were used as input to and for verification of dosage and reacidification models (DePinto et al. 1989).

This paper summarizes the results of the Geological Survey's hydrologic investigation of Woods Lake and Cranberry Pond from January 1984 through September 1986. It describes the physical and hydrologic characteristics of both lakes and their watersheds, the methods of data collection and analysis, and the calculation and results of the hydrologic balance. It also

[1]This is part of a series of 13 papers devoted to the Lake Acidification Mitigation Project.

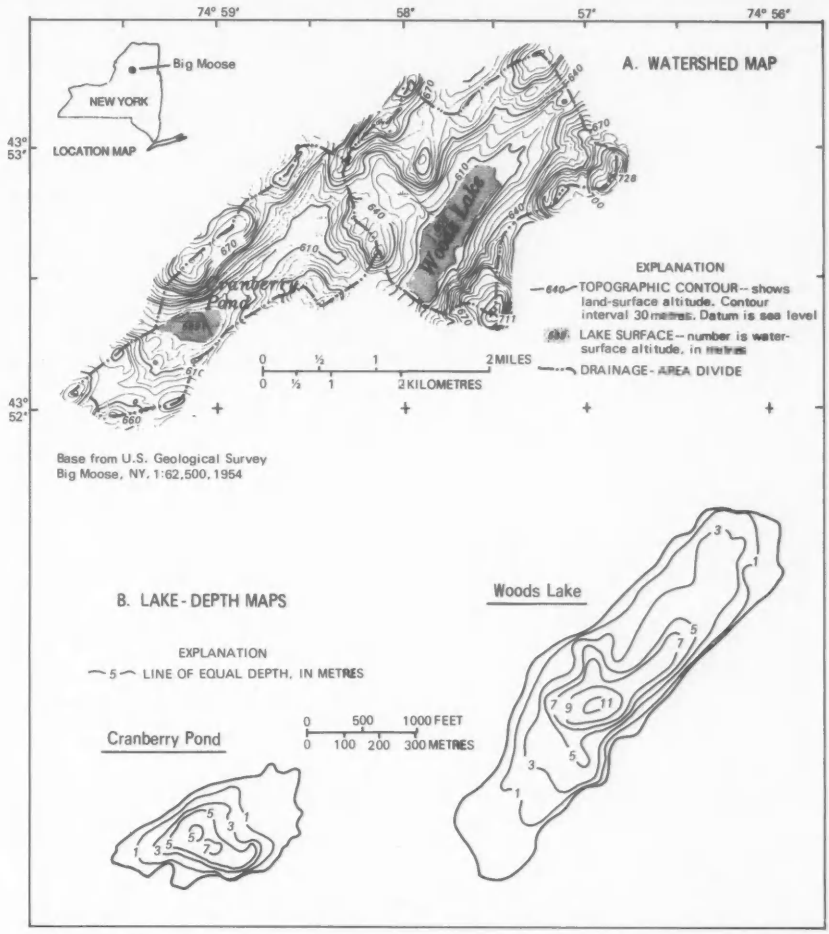


FIG. 1. (A) Location and major physiographic features of Woods Lake and Cranberry Pond, (B) Lake-depth contours.

presents an analysis of the potential errors in the calculation of the hydrologic balance.

## Site Description

Woods Lake and Cranberry Pond are small, acidic (pH 4 to 5) lakes in two adjacent headwater basins in the west-central Adirondack region of New York State (Fig. 1). This area is characterized by forested, rugged terrain that has been subjected to repeated glaciation and is mantled by drift and eolian deposits of variable thickness. The area contains many lakes and wetlands that formed in depressions through glacial scouring and the obstruction of valleys by drift.

Woods Lake is larger and deeper than Cranberry Pond and has nearly four times the volume (Table 1 and Fig. 1). The two watersheds also differ in drainage morphology, although the lakes have comparable contributing drainage areas. Nearly 70% of the Woods Lake watershed is drained by seven perennial streams; the remaining 30% drains directly to the lake. About 91% of the Cranberry Pond watershed is drained by two perennial streams, and the remaining 9% drains directly to the lake. Both lakes are bordered by wetlands. Wetlands at Cranberry Pond occupy a relatively larger area, 1 ha, and become almost fully submerged at the highest lake levels.

The two watersheds are underlain by poorly fractured granitic gneiss that has little capacity to store and transport groundwater. The bedrock has an irregular "washboard" surface covered by thin, sandy till with a premeability of about $1.1 \times 10^{-3}$ cm·s$^{-1}$. Seismic-refraction surveys indicate that till deposits less than 3 m deep cover 90% of the Woods Lake watershed (April and Newton 1985) and 100% of the Cranberry Pond watershed. The Woods Lake watershed contains an area of thicker till (up to 10 m deep) along the northwest shore of the lake.

Annual precipitation in the vicinity of the study lakes averages 123 cm, and air temperature generally ranges from −40° to 27°C. This area has one of the highest annual precipitation totals in New York State as a result of orographic effects upon prevailing winds from Lake Ontario about 100 km to the west. Approximately 40% of the annual precipitation falls as snow, which accumulates to an average depth of 76.2 cm during winter (Dethier 1966). Melting of the snowpack in the spring causes seasonally high runoff. Evapotranspiration returns approximately 40% of the annual precipitation to the atmosphere (Mur-

TABLE 1. Lake and watershed characteristics of Woods Lake and Cranberry Pond.

| Characteristics | Cranberry Pond | Woods Lake |
|---|---|---|
| Basin area ($km^2$) | 1.55 | 2.07 |
| Lake-surface area ($km^2$) | 0.08 | 0.23 |
| Watershed area (basin area minus lake area, $km^2$) | 1.48 | 1.84 |
| Maximum basin relief (m) | 105 | 122 |
| Forest cover (%) | 93.2 | 98.1 |
| Wetlands (%) | 6.8 | 1.9 |
| Average thickness of surficial deposits (m) | 1.8 | 2.3 |
| Basin area with surficial deposits more than 3 m thick (%) | < 5 | 9.2 |
| Lake volume ($10^5 m^3$) | 2.07 | 8.00 |
| Maximum lake depth (m) | 7.6 | 12 |
| Mean lake depth (m) | 2.9 | 3.5 |
| Lake-surface altitude (m above sea level) | 589 | 606 |
| Ratio of lake area to watershed | 0.05 | 0.13 |
| Average lakewater residence time (d) | 63 | 174 |

doch et al. 1985). Evapotranspiration approximately equals average precipitation during the summer, which results in seasonal low flows.

## Methods

A hydrologic balance, a common method used to describe and compare lake hydrology, was calculated for each lake. The method is based on the conservation of mass and requires that the water gain equal the water loss plus or minus changes in lake storage. Water gain includes surface-water inflow, groundwater inflow, and precipitation, and water loss includes surface-water outflow, groundwater outflow, and evaporation. Groundwater outflow was assumed to be negligible in this study because both lakes have poorly fractured bedrock controls and because measurement of potentiometric head along the lake shore at the lake outlets indicated no groundwater loss.

The hydrologic balance of each lake is based on the equation

$$(1) \quad I = O + E - P + LS,$$

where $I$ = groundwater and surface-water inflow, $O$ = surface-water outflow, $E$ = evaporation, $P$ = precipitation, and $LS$ = change in lake storage.

Daily precipitation was measured by a recording gauge installed in a clearing at Cranberry Pond. The areal distribution of precipitation was measured during ice-free months by seven nonrecording bulk gauges installed throughout both watersheds. The monthly sum of the daily precipitation values measured by the recording gauge was multiplied by the surface area of each lake to calculate the quantity of precipitation falling directly on each lake. The surface area of each lake, determined by planimetering aerial photographs taken in October 1984, was assumed to be a constant value throughout the range of observed lake stages.

Lake evaporation was calculated by three different empirical methods (mass-transfer, saturation vapor pressure, and published values), each of which was used for a different time period. Evaporation during ice-free months was calculated by the mass-transfer method (Harbeck 1962) from meteorologic data recorded at Woods Lake. A mass-transfer coefficient for each lake was calculated from the slope of the best-fit line representing the change in lake stage adjusted for inflow and outflow plotted against the mass-transfer product (Langbein et al. 1951). Because seasonal variations in the magnitude of the mass-transfer coefficient have been reported (Meyboom 1967), data from three periods (April 30 to June 15, June 15 to September 15, and September 15 to October 30) were plotted, and lines of best-fit were calculated for each time period.

The saturation–vapor–pressure method (Hamon 1961) was used to calculate lake evaporation during the first year of the study and in subsequent periods of equipment failure when the mass-transfer method could not be used. This method estimates evaporation on a regional basis from a temperature–dependent, vapor–density function and an adjustment for the mean number of possible daylight hours. The mean number of possible daylight hours for each given period was obtained from a standard table (Gray 1970), and daily mean air-temperature data were obtained from National Weather Service stations at Stillwater Reservoir and at Big Moose, 8 km northwest and 4 km southeast of the study lakes, respectively.

Evaporation during months with partial or complete ice cover, November through April, was derived from regional evaporation estimates reported by the Soil Conservation Service (United States Department of Agriculture 1961) for shallow lakes and reservoirs.

Surface-water outflow was measured at a streamflow-gauging station below the outlet of each lake. Water stage was continually recorded, and a corresponding daily discharge was calculated from a stage–to–discharge relationship (Carter and Davidian 1965; Buchanan and Somers 1965; and Kennedy 1983, 1984). The lake–surface elevation was also continually measured at each lake, and the change in the volume of water stored in the lake was approximated by multiplying the change in lake stage by the surface area of the lake.

Inflow was calculated as the residual of the hydrologic balance. As such, it incorporates errors inherent in the measurement of each component of the equation. The cumulative effect of these errors on the resulting inflow value was calculated by a first-order error analysis (LaBaugh 1985), and the degree of error assigned to each component of the balance was derived from Winter (1981).

The percentages of inflow derived from groundwater inflow and from surface-water inflow were estimated. Estimates of surface-water inflow were based on continual measurement of discharge during ice-free periods at a streamflow–gauging station at a tributary to Woods Lake and approximately monthly measurements of instantaneous discharge at all tributaries to each lake. Groundwater inflow to the lakes was estimated by subtracting the estimated surface-water inflow from the total calculated inflow.

Groundwater inflow to Woods Lake also was calculated from measurements of potentiometric head and hydraulic conductivity. Potentiometric head was measured with a portable potentiomanometer (Winter et al. 1988) at approximately 60 sites along 15 transects in the littoral zone at 6- to 8-wk intervals during the ice-free months. From these values and a mean value of hydraulic conductivity, the rate of groundwater seepage was calculated with Darcy's equation and applied to the zone of active seepage as described by McBride and Pfannkuch (1975) to obtain total seepage into Woods Lake. The mean hydraulic conductivity of the littoral zone bottom sediments was derived

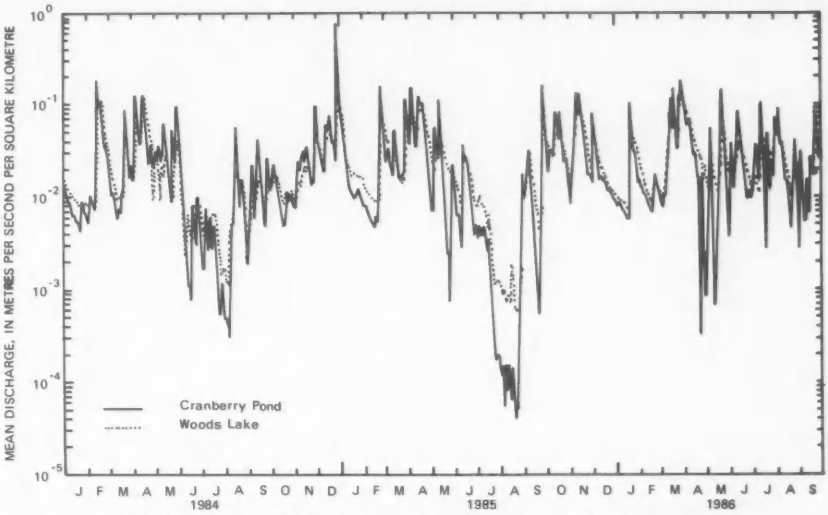


FIG. 2. Outlet hydrographs of Woods Lake and Cranberry Pond, adjusted for drainage area.

TABLE 2. Estimated surface-water and groundwater inflow to Woods Lake and Cranberry Pond. All values are in thousands of cubic meters.

| Month | Ground water | Surface water | Total | Ground water | Surface water | Total |
|---|---|---|---|---|---|---|
| | Woods Lake | | | Cranberry Pond | | |
| | | | *1985* | | | |
| May | | | | 7.10 | 84.40 | 91.50 |
| June | 40.50 | 34.50 | 75.00 | 9.80 | 30.50 | 40.30 |
| July | 20.40 | 6.70 | 27.10 | 7.01 | 1.34 | 8.35 |
| August | 3.96 | 8.04 | 12.00 | 0.49 | 9.91 | 10.40 |
| September | 15.00 | 106.00 | 121.00 | 13.20 | 59.90 | 73.10 |
| October | 46.00 | 108.00 | 154.00 | 27.80 | 96.20 | 124.00 |
| November | 49.00 | 159.00 | 208.00 | 26.20 | 135.80 | 162.00 |
| December | 40.70 | 52.20 | 92.90 | 15.40 | 46.60 | 62.00 |
| | | | *1986* | | | |
| January | 26.50 | 75.50 | 102.00 | 7.70 | 65.90 | 73.60 |
| February | 10.90 | 31.50 | 42.40 | 3.30 | 24.70 | 28.00 |
| March | 58.00 | 279.00 | 337.00 | 23.00 | 217.00 | 240.00 |
| April | 65.00 | 146.00 | 211.00 | 29.00 | 102.00 | 131.00 |
| May | 43.40 | 81.60 | 125.00 | 12.90 | 79.80 | 92.70 |
| June | 44.70 | 64.30 | 109.00 | 18.90 | 53.70 | 72.60 |
| July | 54.50 | 90.50 | 145.00 | 32.00 | 102.00 | 134.00 |
| August | 60.00 | 64.00 | 124.00 | 23.20 | 82.80 | 106.00 |
| September | 30.20 | 72.80 | 103.00 | 6.60 | 73.10 | 79.70 |
| Average | 38.10 | 86.20 | 124.30 | 15.50 | 74.50 | 90.00 |
| Percent total inflow | 31 | 69 | — | 17 | 83 | — |

from 15 point measurements of seepage made by seepage meters (Lee 1977) and measurements of potentiometric head in the bottom sediments at the same locations. These measured values were applied to Darcy's equation to obtain point values of hydraulic conductivity, and the mean hydraulic conductivity value was calculated.

## Results

### Hydrologic Characteristics

The physiographic and climatic similarity between the two lake systems gives them similar hydrologic characteristics. Because the lakes lie within adjacent drainage basins at nearly equal elevations, the quantity and spatial distribution of precipitation in the two basins was uniform. The average precipitation during the nonwinter period in 1984 and 1985 in the Woods Lake watershed was 83.0 cm, nearly identical to the 83.2 cm in the Cranberry Pond watershed, and monthly precipitation in individual bulk and recording gauges in both basins generally agreed within 10%.

With nearly equal precipitation, long-term discharge from the lake basins was also similar. Average outflows during the

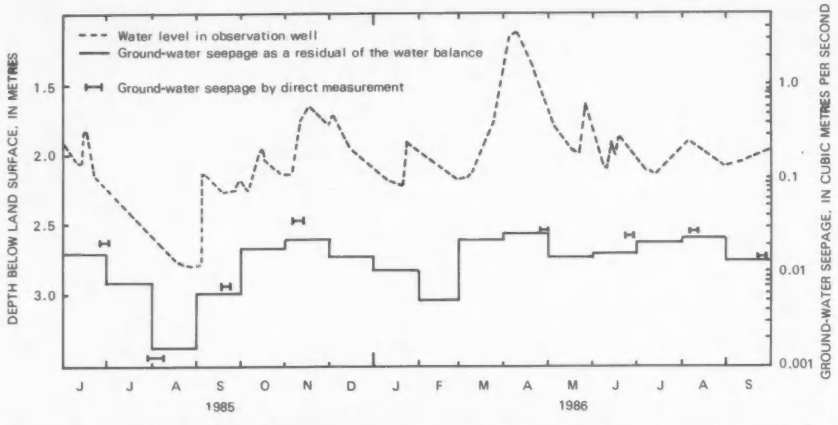


FIG. 3. Measured and estimated groundwater seepage to Woods Lake and groundwater levels recorded in observation well in the Woods Lake watershed.

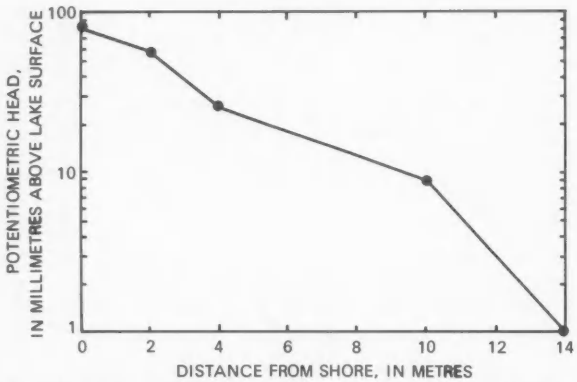


FIG. 4. Potentiometric-head readings from a typical transect at Woods Lake.

study were 0.0378 $m^3 \cdot s^{-1}$ from Cranberry Pond and 0.0523 $m^3 \cdot s^{-1}$ from Woods Lake. Adjusted for drainage area, the outflows were 0.0243 $m^3 \cdot s^{-1} \cdot km^{-2}$ for Cranberry Pond and 0.0254 for Woods Lake.

The thickness of unconsolidated deposits overlying bedrock has a marked effect on the flow paths and hydrologic response of the basins. The thin deposits in the lake watersheds have little capacity to store and transmit groundwater; as a result, the flow system is shallow and dynamic and responds quickly to precipitation. In these watersheds, water moves quickly to the lake as surface runoff, interflow, or shallow groundwater seepage, which produces "flashy" hydrographs with high peak flows and poorly sustained base flows. The outflow hydrographs in Fig. 2, which show seasonal trends of high flows in early spring and late fall and low flows in summer, also indicate that runoff from both lakes is highly variable during all seasons as a result of the rapid response to precipitation.

The hydrograph for the Woods Lake outlet is less "flashy" than that for Cranberry Pond (Fig. 2) because Woods Lake has a larger surface area and a larger ratio of lake-storage capacity to inflow. The Woods Lake watershed also contains small but relatively thick, permeable sandy till deposits that have the capacity to store groundwater and gradually release it as seepage. These factors cause smaller peak flow during storms and slightly greater sustained base flow during dry periods at Woods Lake outlet. The mean daily discharge measured at the lake outlets ranged from $5.7 \times 10^{-5}$ to 1.05 $m^3 \cdot s^{-1}$ at Cranberry Pond and from $1.1 \times 10^{-3}$ to 0.88 $m^3 \cdot s^{-1}$ at Woods Lake.

Both watersheds are surface-water dominated systems. Surface-water inflow constituted 69% of the total inflow to Woods Lake and 84% of the total inflow to Cranberry Pond (Table 2). The percentage of total inflow to each lake that consists of surface-water appears to be controlled by the drainage morphology of the watershed; 70% of the Woods Lake watershed and 91% of Cranberry Pond watershed are drained by perennial streams that contribute nearly all the surface-water inflow to the lakes. Water in the remaining areas drains directly to the lakes as interflow and groundwater seepage. Little overland flow enters the lakes from the area of direct drainage, except during periods of snowmelt, because the precipitation intensity rarely exceeds the infiltration capacity of the surficial deposits (Murdoch et al. 1985).

Groundwater seepage, as calculated from the residual of the water balance, constituted 31% of the total inflow to Woods Lake and 16% of the total inflow to Cranberry Pond. Seepage calculated at Woods Lake from measurements of potentiometric head and hydraulic conductivity equaled about 38% of the total inflow to Woods Lake; this value agrees with the value calculated from the residual of the water balance equation and, again, is nearly equal to the proportion of the watershed area that drains directly to the lake. This indicates that groundwater seepage to Woods Lake largely follows the surface topography as a local flow system in the area of direct drainage to the lake.

The unconsolidated deposits in the area of direct drainage to both lakes are generally less than 3 m thick, except along the northwestern shore of Woods Lake, where they are as much as 10 m thick. As a result, groundwater flows in a shallow system, and seepage fluctuates rapidly in response to precipitation and recharge, as evidenced by groundwater levels measured in the area of direct drainage (Fig. 3). Seepage declined rapidly at Woods Lake during the dry summer of 1985 but quickly increased in response to precipitation in late August and early September. Seepage calculated by measurements of potentiometric head and hydraulic conductivity at Woods Lake

TABLE 3. Monthly hydrologic balance for Woods Lake with potential errors of calculated inflow, 1984–86. All values are in cubic metres. Values in parentheses are the potential error of calculated inflow. Negative values of lake storage indicate water going into storage.

| Month | Outflow | Evaporation | Precipitation | Lake storage | Inflow |
|---|---|---|---|---|---|
| | | | *1984* | | |
| January | 55 400 | 2 150 | 13 400 | −11 800 | 32 350 (8 830) |
| February | 212 000 | 2 150 | 20 700 | 23 600 | 217 050 (32 200) |
| March | 93 400 | 4 050 | 13 200 | −11 800 | 72 450 (14 300) |
| April | 280 000 | 7 820 | 22 800 | −9 020 | 256 000 (42 300) |
| May | 115 000 | 14 400 | 31 900 | 710 | 98 210 (18 900) |
| June | 39 400 | 22 900 | 19 000 | −8 340 | 34 960 (9 860) |
| July | 25 500 | 26 100 | 24 900 | −4 860 | 21 840 (10 100) |
| August | 41 600 | 24 100 | 35 800 | 22 300 | 52 200 (11 900) |
| September | 56 400 | 11 400 | 22 500 | −7 640 | 37 660 (10 200) |
| October | 69 800 | 8 350 | 11 000 | −5 540 | 61 610 (11 000) |
| November | 92 900 | 5 780 | 23 200 | 31 300 | 106 780 (14 800) |
| December | 313 000 | 2 150 | 66 000 | 42 400 | 291 550 (48 800) |
| Calculated year total | 1 394 400 | 131 350 | 304 400 | 61 310 | 1 282 660 (141 000) |
| | | | *1985* | | |
| January | 178 000 | 2 150 | 17 400 | −73 700 | 89 050 (27 900) |
| February | 104 000 | 2 150 | 20 800 | 48 000 | 133 350 (16 800) |
| March | 186 000 | 4 050 | 23 800 | −670 | 165 580 (28 300) |
| April | 345 000 | 7 020 | 15 100 | −30 600 | 306 320 (52 000) |
| May | 146 000 | 16 500 | 26 600 | −13 200 | 122 700 (23 100) |
| June | 86 800 | 18 200 | 20 300 | −9 700 | 75 000 (14 700) |
| July | 27 100 | 25 500 | 15 100 | −10 400 | 27 100 (9 220) |
| August | 7 100 | 17 500 | 25 100 | 12 500 | 12 000 (7 450) |
| September | 106 000 | 12 300 | 38 200 | 41 000 | 121 100 (18 500) |
| October | 204 000 | 7 190 | 23 300 | −33 400 | 154 490 (31 200) |
| November | 238 000 | 5 800 | 38 200 | 2 780 | 208 380 (36 600) |
| December | 116 000 | 2 150 | 19 700 | −5 540 | 92 910 (17 900) |
| Calculated year total | 1 744 000 | 120 510 | 283 600 | −72 930 | 1 507 980 (176 000) |
| | | | *1986* | | |
| January | 110 000 | 2 150 | 20 800 | 10 400 | 101 750 (17 100) |
| February | 65 800 | 2 150 | 14 500 | −11 100 | 42 350 (10 400) |
| March | 268 000 | 4 050 | 23 800 | 89 000 | 337 250 (41 500) |
| April | 289 000 | 9 400 | 15 600 | −71 600 | 211 200 (44 200) |
| May | 144 000 | 18 700 | 24 300 | −13 900 | 124 500 (22 900) |
| June | 127 000 | 19 600 | 33 600 | −4 150 | 108 850 (21 000) |
| July | 146 000 | 23 500 | 48 500 | 23 600 | 144 600 (25 100) |
| August | 154 000 | 22 800 | 30 500 | −22 300 | 124 000 (25 000) |
| September | 99 500 | 13 700 | 24 300 | 13 900 | 102 800 (16 300) |
| Jan. to Sept. total | 1 403 300 | 116 050 | 235 900 | 13 850 | 1 297 300 (142 000) |

ranged from 0.0011 $m^3 \cdot s^{-1}$ in August 1985 to 0.0345 $m^3 \cdot s^{-1}$ in November 1985.

The thin unconsolidated deposits at Woods Lake also result in a relatively narrow zone of active seepage. Seepage velocity measured at individual sites at Woods Lake ranged from $2 \times 10^{-3}$ to $2 \times 10^{-7}$ $cm \cdot s^{-1}$. If a uniform hydraulic conductivity is assumed, seepage decreased exponentially with distance from the shore (Fig. 4) at an average of two orders of magnitude within 13 m. Similar patterns were observed in the field by Mann and McBride (1972), John and Lock (1977), and Lee (1977) and were theoretically predicted by McBride and Pfannkuch (1975), who showed that the width of the zone of rapid seepage is controlled in part by the depth of the permeable material along the lakeshore.

The flow system through which groundwater enters a lake largely affects the hydrology and water chemistry of the lake. Lake basins with deep flow systems tend to have greater capacity to store groundwater, which moderates peak flows and sustains base flows. Water in deep flow systems also has a longer residence time, during which neutralizing reactions, such as primary mineral weathering, can proceed toward equilibrium (April and Newton 1985). In contrast, lake basins with shallow flow systems, such as Woods Lake and, even more so, Cranberry Pond, tend to have variable rates of groundwater flow and relatively short groundwater residence times. Neutralization of acidic waters in these systems is incomplete, and the contribution of groundwater to the lakewater acid-neutralizing capacity is small. Lake basins with shallow flow systems can, therefore, be expected to reacidify quickly after base addition.

## Hydrologic Balance

The hydrologic balance developed for each lake indicates that the lakes are similar in the seasonal distribution of inflow and

TABLE 4. Monthly hydrologic balance for Cranberry Pond with potential errors of calculated inflows, 1984–86. All values are in cubic metres. Values in parentheses are the potential error of calculated inflow. Negative values of lake storage indicate water going into storage.

| Month | Outflow | Evaporation | Precipitation | Lake storage | Inflow | |
|---|---|---|---|---|---|---|
| | | | *1984* | | | |
| January | 29 100 | 760 | 4 720 | −2 200 | 22 940 | (4 470) |
| February | 159 000 | 760 | 7 300 | 6 140 | 158 600 | (23 800) |
| March | 74 600 | 1 440 | 4 460 | −3 440 | 68 140 | (11 200) |
| April | 195 000 | 2 780 | 8 060 | 3 910 | 193 630 | (29 300) |
| May | 132 000 | 5 070 | 11 300 | 6 880 | 132 650 | (20 000) |
| June | 32 700 | 8 100 | 6 700 | −14 200 | 19 900 | (5 810) |
| July | 12 200 | 9 230 | 8 770 | −3 440 | 9 220 | (3 770) |
| August | 42 700 | 8 520 | 12 700 | 2 690 | 41 210 | (7 340) |
| September | 54 600 | 4 020 | 7 950 | −730 | 49 940 | (8 430) |
| October | 41 700 | 2 940 | 3 870 | −2 200 | 38 570 | (6 350) |
| November | 89 500 | 2 040 | 8 170 | 14 700 | 98 070 | (13 600) |
| December | 265 000 | 760 | 23 400 | −730 | 241 630 | (40 100) |
| Calculated year total | 1 128 100 | 46 420 | 107 400 | 7 380 | 1 074 500 | (113 000) |
| | | | *1985* | | | |
| January | 87 100 | 760 | 6 130 | −14 700 | 67 030 | (13 100) |
| February | 77 300 | 760 | 7 350 | 8 830 | 79 540 | (11 700) |
| March | 129 000 | 1 440 | 8 400 | 6 400 | 128 440 | (19 500) |
| April | 247 000 | 2 490 | 5 310 | −12 800 | 231 380 | (37 000) |
| May | 94 200 | 4 960 | 9 420 | 1 730 | 91 470 | (14 300) |
| June | 45 300 | 6 820 | 7 150 | −4 660 | 40 310 | (7 260) |
| July | 8 810 | 9 030 | 5 310 | −4 180 | 8 350 | (3 220) |
| August | 3 540 | 7 390 | 8 880 | 8 350 | 10 400 | (3 010) |
| September | 77 000 | 4 620 | 13 500 | 4 930 | 73 050 | (12 000) |
| October | 136 000 | 2 610 | 8 230 | −6 870 | 123 510 | (20 500) |
| November | 173 000 | 2 040 | 13 500 | 480 | 162 020 | (26 100) |
| December | 70 900 | 760 | 6 980 | −2 710 | 61 970 | (10 700) |
| Calculated year total | 1 149 150 | 43 680 | 100 160 | −15 200 | 1 077 470 | (115 000) |
| | | | *1986* | | | |
| January | 77 500 | 760 | 7 350 | 2 720 | 73 630 | (11 700) |
| February | 34 100 | 760 | 5 120 | −1 720 | 28 020 | (5 230) |
| March | 226 000 | 1 440 | 8 400 | 21 100 | 240 140 | (34 000) |
| April | 144 000 | 3 340 | 5 510 | −10 600 | 131 230 | (21 700) |
| May | 93 200 | 6 600 | 8 600 | 1 470 | 92 670 | (14 200) |
| June | 86 700 | 6 940 | 11 900 | −9 110 | 72 630 | (13 400) |
| July | 122 000 | 8 500 | 17 100 | 20 900 | 134 300 | (18 900) |
| August | 121 000 | 8 830 | 10 800 | −13 500 | 105 530 | (18 600) |
| September | 86 100 | 5 320 | 8 570 | −3 160 | 79 690 | (13 100) |
| Jan. to Sept. total | 990 600 | 42 490 | 83 350 | 8 100 | 957 840 | (98 900) |

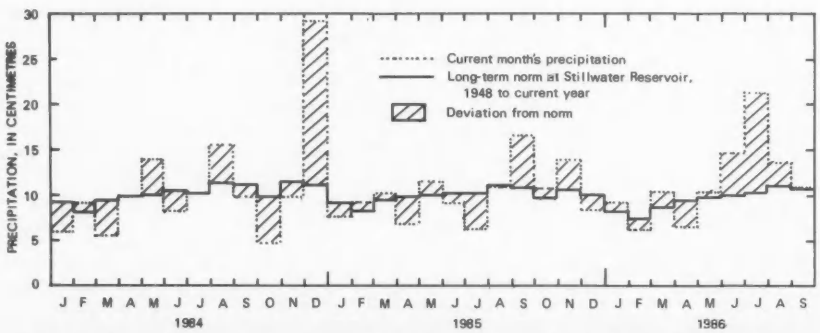


FIG. 5. Monthly precipitation measured at Cranberry Pond and deviation from long-term norm.

TABLE 5. Potential errors of annual inflow to Woods Lake and Cranberry Pond calculated from the hydrologic balance, 1984–86. Volume and errors are in thousands of cubic metres. Numbers in parentheses are estimated percent error.

| | 1984 | | 1985 | | 1986 | |
|---|---|---|---|---|---|---|
| Component | Volume | Error | Volume | Error | Volume | Error |
| | | | *Cranberry Pond* | | | |
| Outflow (10) | 1 130 | 113 | 1 150 | 115 | 991 | 99.1 |
| Precipitation (5) | 107 | 5.4 | 100 | 5.0 | 83.4 | 4.2 |
| Evaporation (15) | 46.4 | 7.0 | 43.7 | 6.6 | 42.5 | 6.4 |
| Lake storage (10) | 7.4 | .7 | −15.2 | 1.5 | 8.1 | .8 |
| Inflow | 1 070 | 113 | 1 080 | 115 | 958 | 99.4 |
| Inflow error (percent) | 10.6 | | 10.6 | | 10.4 | |
| | | | *Woods Lake* | | | |
| Outflow (10) | 1 390 | 139 | 1 740 | 174 | 1 400 | 140 |
| Precipitation (5) | 304 | 15.2 | 284 | 14.2 | 236 | 11.8 |
| Evaporation (15) | 131 | 19.7 | 121 | 18.2 | 116 | 17.4 |
| Lake storage (10) | 61.3 | 6.1 | −72.9 | 7.3 | 14.0 | 1.4 |
| Inflow | 1 280 | 141 | 1 510 | 176 | 1 300 | 142 |
| Inflow error (percent) | 11 | | 11.7 | | 10.9 | |

TABLE 6. Potential errors of monthly inflow calculated by the hydrologic balance, Woods Lake, 1984. Volumes and errors are in thousands of cubic metres. Numbers in parentheses are estimated percent error.

| | Outflow (15) | | Precipitation (20) | | Evaporation (30) | | Lake storage (10) | | Inflow | | Percent error |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Volume | Error | Volume | Error | Volume | Error | Volume | Error | Volume | Error | |
| January | 55.4 | 8.31 | 13.4 | 2.68 | 2.15 | 0.65 | 11.8 | 1.18 | 32.4 | 8.83 | 27.3 |
| February | 212.0 | 31.8 | 20.7 | 4.14 | 2.15 | 0.65 | 23.6 | 2.36 | 217.0 | 32.2 | 14.8 |
| March | 93.4 | 14.0 | 13.2 | 2.64 | 4.05 | 1.22 | 11.8 | 1.18 | 72.5 | 14.3 | 19.7 |
| April | 280.0 | 42.0 | 22.8 | 4.56 | 7.82 | 2.35 | 9.02 | 0.90 | 256.0 | 42.3 | 16.5 |
| May | 115.0 | 17.3 | 31.9 | 6.38 | 14.4 | 4.32 | 0.71 | 0.07 | 98.2 | 18.9 | 19.2 |
| June | 39.4 | 5.91 | 19.0 | 3.80 | 22.9 | 6.87 | 8.34 | 0.83 | 35.0 | 9.86 | 28.2 |
| July | 25.5 | 3.83 | 24.9 | 4.98 | 26.1 | 7.83 | 4.86 | 0.49 | 21.8 | 10.1 | 46.3 |
| August | 41.6 | 6.24 | 35.8 | 7.16 | 24.1 | 7.23 | 22.3 | 0.22 | 52.2 | 11.9 | 22.8 |
| September | 56.4 | 8.46 | 22.5 | 4.50 | 11.4 | 3.42 | 7.64 | 0.76 | 37.7 | 10.2 | 27.1 |
| October | 69.8 | 10.5 | 11.0 | 2.20 | 8.35 | 2.51 | 5.54 | 0.55 | 61.6 | 11.0 | 17.9 |
| November | 92.9 | 13.9 | 23.2 | 4.64 | 5.78 | 1.73 | 31.3 | 0.31 | 107.0 | 14.8 | 13.8 |
| December | 313.0 | 47.0 | 66.0 | 13.2 | 2.15 | 0.65 | 42.4 | 0.42 | 292.0 | 48.8 | 16.7 |

outflow and in the relative contribution of the individual components of the balance (Tables 3 and 4). The annual surface-water outflow from each lake nearly equaled the annual inflow of surface water and groundwater; the relatively minor differences are attributed to change in lake storage, evaporation, and precipitation.

Precipitation on the lake surface during the study equaled about 20% of the total water gain to Woods Lake and 9.4% of the total gain to Cranberry Pond; evaporation equaled 7.7% of the water loss from Woods Lake and 3.9% from Cranberry Pond. Changes in lake storage were negligible on an annual basis and over the 33-mo study period. Precipitation and evaporation represent a larger portion of the hydrologic balance at Woods Lake than at Cranberry Pond because Woods Lake has a larger ratio of lake surface area to drainage area than does Cranberry Pond.

Evaporation, precipitation, and change in lake storage may constitute a larger component of the monthly balance than of the annual balance. Lake storage averaged 6.5 and 15% of the total monthly outflows of Cranberry Pond and Woods Lake, respectively. During the summer, when evapotranspiration in the watersheds equaled or exceeded precipitation, the inflows to and outflows from the lakes were greatly diminished. Precipitation and evaporation constitute more than 50% of the monthly water gain or loss from the lakes during the summer months of 1984 and 1985.

The variability of precipitation (Fig. 5) caused monthly inflows to and outflows from the lakes to fluctuate by as much as an order of magnitude over a given year (Tables 3 and 4), which resulted in variable hydraulic retention times. The average hydraulic retention time of Cranberry Pond during the study was 63 d and ranged from less than 30 d during spring snowmelt in 1986 to more than 150 d during the summer and early fall of 1984. The average hydraulic retention time at Woods Lake over the study was 174 d and ranged from about 120 d during the winter and spring of 1985 to about 270 d during the spring and fall of 1984.

These hydraulic retention times may be somewhat less than what might be expected over the long term. The total precipitation of 383 cm measured during the study was 8.9% greater than the long-term normal determined from the nearby U.S. Weather Service stations at Stillwater Reservoir (National

Oceanic and Atmospheric Administration, monthly climatological data). Precipitation during the 17 mo before base addition, January 1984 to May 1985, was 5% greater than normal, and precipitation after base addition was 13.2% greater than normal. Greater than normal precipitation after base addition would increase the flushing rate and accelerate reacidification.

### Error Analysis

Calculated inflow incorporates the errors inherent in the measurements and analyses of the individual components of the hydrologic balance. The total error of the balance depends on the accuracy of the individual-component values, the proportion that these components contribute to the total balance, and the degree to which positive and negative errors cancel. Because positive and negative errors are assumed to be randomly distributed, the total error associated with an individual component and with the balance as a whole will diminish as the period of record increases. Thus, a hydrologic balance calculated for a full year will be more accurate than a balance calculated for any part of the year.

The potential error in the annual balance for each lake ranged from 10% to 12% (Table 5), whereas the potential error in the monthly balance ranged from 14 to 46% (Table 6). The largest monthly potential errors were during the summer, when evaporation (which could not be measured with great accuracy) formed a relatively large part of the balance; the potential error was least during the early spring and late fall, when surface-water outflow (which could be measured more accurately) formed a larger part of the balance. The relatively low potential error in the annual balance results from the relatively large part of the annual balance formed by surface-water outflow.

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# Survival, Growth, Reproduction, and Diet of Brook Trout (*Salvelinus fontinalis*) Stocked into Lakes after Liming to Mitigate Acidity[1]

Steven P. Gloss[2], Carl L. Schofield, Robert L. Spateholts[3], and Barbara A. Plonski

*Cooperative Fish and Wildlife Research Unit, U.S. Fish and Wildlife Service, Department of Natural Resources, Cornell University, Ithaca, NY 14853, USA*

Gloss, S. P., C. L. Schofield, R. L. Spateholts, and B. A. Plonski. 1989. Survival, growth, reproduction, and diet of brook trout (*Salvelinus fontinalis*) stocked into lakes after liming to mitigate acidity. Can. J. Fish. Aquat. Sci. 46: 277–286.

Brook trout (*Salvelinus fontinalis*) were stocked into two previously acidic (pH 4.5–5.2) Adirondack Mountain lakes, Woods Lake and Cranberry Pond, following liming in June, 1985. Age 0+ Temiscamie × Domestic hybrid brook trout were stocked at 200·ha$^{-1}$ with one-half of the fish selected for presumed acid tolerance. Age 1+ Temiscamie strain brook trout were also stocked at 50·ha$^{-1}$. Liming increased pH to well above 7 and alkalinity to over 200 μeq·L$^{-1}$. Growth and condition of stocked fish were good while water quality conditions remained suitable. However, in Cranberry Pond, which reacidified 6 mo after liming, both growth and survival declined dramatically. Much of the population loss was due to emigration. Annual survival in Woods Lake averaged 35 and 25% for the age 0+ and 1+ fish, respectively. Initially large invertebrates made up most of the diet for stocked fish. These taxa were replaced by zooplankton within a few months. Limited natural reproduction was associated with low velocity groundwater inflows and high acidity in tributary streams. Fry emergence from artificial spawning substrates placed in Woods Lake peaked well after snowmelt inflows which produced toxic conditions in littoral areas.

On a ensemencé des ombles de fontaine (*Salvelinus fontinalis*) dans le lac Woods et l'étang Cranberry, deux lacs acidifiés des Adirondacks (pH : 4,5–5,2) traités avec une base neutralisante en juin 1985. Les ombles de fontaine d'ensemencement étaient des hybrides Temiscamie × Domestic de classe d'âge 0+; on en a lâché 200 par hectare et la moitié des poissons avaient été sélectionnés pour leur tolérance présumée à l'acide. On a aussi lâché des ombles de fontaine de souche Temiscamie de classe d'âge 1+ à raison de 50 par hectare. Par suite du traitement à la base, le pH est monté bien au-dessus de 7 et l'alcalinité, à plus de 200 μeq·L$^{-1}$. La croissance et l'état général des poissons d'ensemencement ont été satisfaisants tant que la qualité de l'eau est restée bonne. Toutefois, dans l'étang Cranberry, réacidifié 6 mo après le traitement, la croissance et la survie des poissons ont baissé de façon spectaculaire. La plus grande partie de la baisse de la population est due à la migration. Dans le lac Woods, le taux de survie annuel moyen était de 35 % pour les poissons de la classe d'âge 0+ et de 25 % pour les poissons de la classe d'âge 1+. Au début, les poissons d'ensemencement se sont surtout nourris d'invertébrés de grande taille. Ces derniers ont été remplacés par le zooplancton au bout de quelques mois. On a constaté que la reproduction naturelle était limitée : ce phénomène est lié à la vitesse réduite des entrées d'eau souterraine ainsi qu'à la grande acidité des eaux des tributaires. L'émergence des alevins du substrat de reproduction artificiel qu'on a placé dans le lac Woods a culminé longtemps après l'arrivée des eaux de fonte, apport qui a rendu le milieu toxique dans les zones littorales.

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The effects of surface water acidification on fish have been described by numerous authors and include loss of complete populations from acidic lakes in certain geographical areas (Schofield 1982; Harvey and Lee 1982), direct toxicity to fish (Baker and Schofield 1981), physiological changes (Wood and McDonald 1982), and potential for episodic toxicity to early life stages under field conditions (Gunn 1986). The mitigation of acidification effects in lakes has been attempted primarily through the addition of calcium carbonate ($CaCO_3$) directly to the water column (Driscoll et al. 1982; Hultberg and Andersson 1982; Lindstrom et al. 1984; Wright 1985). The principal purpose of liming lakes is either to maintain or restore water quality conditions suitable for survival of fish populations. Most chronically acidified lakes (pH 4.5–5.0) have already lost any fish populations which were previously present so it is necessary to reintroduce fish after liming in these systems. Reintroductions of brown trout (*Salmo trutta*) and Arctic char (*Salvelinus salvelinus*) populations following liming have been described for Swedish lakes (Hultberg and Andersson 1982; Hasselrot et al. 1984; Lindstrom et al. 1984). The effects of liming on existing populations of yellow perch (*Perca flavescens*) and lake trout (*Salvelinus namaycush*) (Booth et al. 1986) in Canada and perch (*P. fluviatalis*) and roach (*Rutilus rutilus*) in Swedish lakes have been generally favorable (Nyberg et al. 1986). However, only scanty information is available in

[1]This is part of a series of 13 papers devoted to the Lake Acidification Mitigation Project.

[2]Present address: Wyoming Water Research Center, P.O. Box 3067, University Station, University of Wyoming, Laramie, WY 82071, USA.

[3]Present address: Utah Division of Wildlife Resources, P.O. Box 349, Heber City, UT 84032, USA.

TABLE 1. Numbers of brook trout (*Salvelinis fontinalis*) stocked in Woods Lake and Cranberry Pond after liming in June 1985, where $T$ = Temiscamie strain, $T \times D$ = Temiscamie × Domestic hybrid, and $T \times D(s)$ = Temiscamie × Domestic hybrid selected for acid tolerance (see Flick and Webster 1982).

| | Age 1+ | Age 0+$T \times D$ | Age 0+$T \times D(s)$ |
|---|---|---|---|
| Woods Lake | 1200 | 2500 | 2500 |
| Cranberry Pond | 400 | 1000 | 1000 |

the published literature regarding fish reintroductions following liming in the United States (Blake 1981; Kretser and Colquhoun 1984). Numerous small lakes in the Adirondack Mountains of New York have lost fish populations as a result of acidification (Schofield 1982) and current estimates suggest that at least several hundred lakes with relatively low pH (<5.0) are fishless (Schofield et al. 1986). The primary indigenous salmonid species to these small high elevation lakes is the brook trout (*Salvelinus fontinalis*). Our objectives are to describe the survival, growth, reproduction, and diet of reintroduced brook trout during the first 18 mo following liming of two acid lakes. We evaluated two ages and two groups of a hybrid strain of brook trout with respect to survival, growth, and emigration. One group of fish was selected for presumed acid tolerance. Knowledge of the responses of reintroduced fish populations following liming and during reacidification is essential in evaluating the potential for rehabilitating acidified aquatic ecosystems. These data also will be useful in determining the likelihood of successful fish reintroductions if lake chemistry is changed due to a reduction in acidic deposition.

## Materials and Methods

Woods Lake and Cranberry Pond(25 and 7 ha, respectively) were neutralized by the addition of $CaCO_3$ to the water column in late May of 1985 as part of the Lake Acidification Mitigation Project (Porcella 1989). Staubitz and Zarriello (1989) and DePinto et al. (1989) described basin characteristics and liming procedures. Prior to liming, these lakes were chronically acidified with pH's ranging from 4.5 to 5.2 and typically zero or negative alkalinity (Driscoll et al. 1989). Gloss et al. (1987) described the preneutralization fishery status of these lakes indicating both were fishless but that each had previously supported brook trout populations. Furthermore, survival potential for brook trout was either nonexistent (Cranberry Pond) or extremely poor (Woods Lake) prior to liming.

Fish for stocking were obtained from private hatcheries in the Adirondacks. Both lakes were stocked with age 0+ and 1+ brook trout following liming (Table 1). The origins and selection procedures for these groups of fish have been described by Webster and Flick (1981) and Flick et al. (1982). The 1+ Temiscamie strain fish (1+$T$) stocked in Woods Lake were marked with individually numbered jaw tags except for a growth reference group of 100 fish which were introduced unmarked. The age 0+ unselected domestic fish (0+$T \times D$) were given an adipose fin clip in both lakes to differentiate them from those fish selected for acid tolerance (0+$T \times D(s)$). Age 1+ fish were unmarked in Cranberry Pond because of its anticipated rapid reacidification. Population size and survival of stocked fish were estimated from trap net (1.2 m deep, 30 m lead with 1.3-cm mesh, 1.6-m wings with 0.6-cm mesh trap) catches during approximately 4-wk periods in the spring and fall of each year. Population estimates were calculated by the

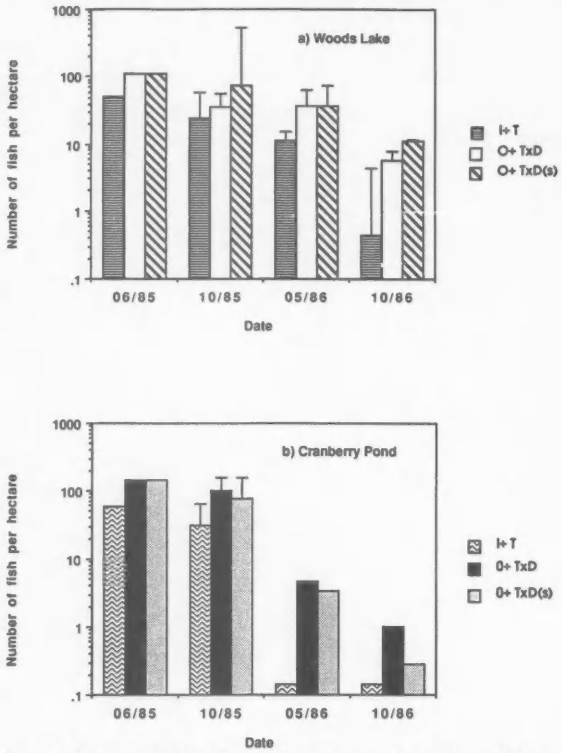


FIG. 1. Spring and fall abundance estimates with 95% confidence intervals for cohorts of brook trout stocked in (a) Woods Lake and (b) Cranberry Pond June 1985 – October 1986 (1+, 0+ = age at stocking; $T$, $T \times D$, $T \times D(s)$ = strain and group.

Schnabel procedure (Ricker 1975) and survival was estimated by ratio of successive seasonal estimates. Survival for the 1+ cohort stocked in Woods Lake with jaw tags was also estimated by Jolly–Seber (Seber 1982). Individual fish were weighed to the nearest gram, measured to the nearest millimetre (total length), examined for marks, given temporary caudal fin clips to detect recaptures within each estimation period, and had scale samples removed prior to release. Scales were later read for age–growth analyses and length-at-age back calculated according to the traditional Lee method (Carlander 1981).

To examine emigration as a possible source of population loss, we constructed inclined screen traps at the outlets of both lakes. Live boxes attached to these traps were monitored approximately every other day during high flow periods (runoff events) and at least every 3 wk otherwise. Adult fish which were in good condition were jaw tagged if previously unmarked, or noted and returned to the lakes to maximize reproductive potential of the population. Age 0+ fish were released downstream after sampling.

Stomach contents of brook trout <200 mm were determined by conducting monthly diurnal gill netting during May to November after the fish introductions. Nets were typically fished 1–4 h to catch a target number of 10 fish. Fish were removed from the nets, examined for marks, weighed, and measured. Stomachs were removed from fish immediately and preserved in 10% formalin. Stomach contents were removed in the laboratory, prey items were sorted to the lowest practical taxon, counted, and the volume of the total contents was deter-

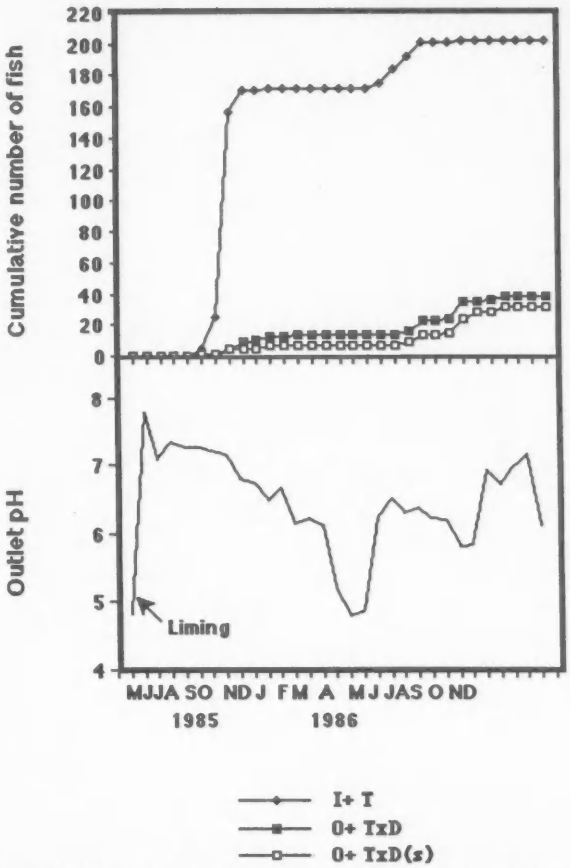


FIG. 2. Outlet pH and emigration pattern of brook trout stocked in Woods Lake following liming in June 1985.

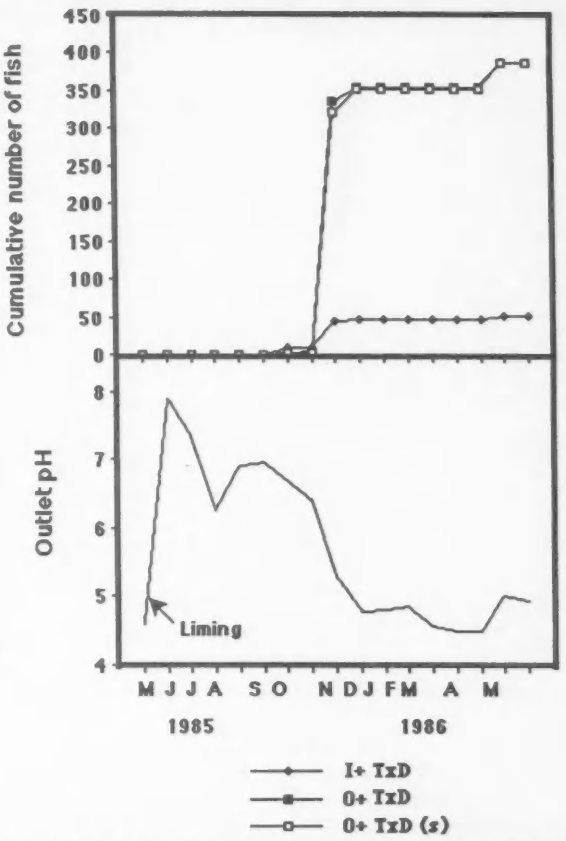


FIG. 3. Outlet pH and emigration pattern of brook trout stocked in Cranberry Pond following liming in June 1985.

mined by water displacement. The relative energy value of major prey taxa was determined using the caloric and biomass values of Swift (1970).

To determine reproductive potential and success we conducted habitat surveys measuring the quality and quantity of groundwater seepage at various sites in Woods Lake with portable peizometers (Staubitz and Zarriello 1989). Analytical measurements were done by Driscoll et al. (1989). Four artificial spawning boxes (2 m × 4 m) were constructed and installed near the primary tributary according to Webster (1962). Each box was divided in half with one 2 × 2 m area of granitic substrate and one of calcareous substrate. Visual inventories of redd construction and spawning activity were made in the fall of each year. One fry emergence trap (Stauffer 1981) was placed over each natural redd just after ice-out. An additional 16 traps were located at random on the spawning boxes (4 each, 2 per substrate type) to quantify emergence.

## Results

### Survival and Growth

Estimated population sizes (Fig. 1) indicated no difference (ANOVA, $p > 0.05$) in the abundance of the selected versus unselected 1985 year-class fish in either Woods Lake or Cranberry Pond 1 yr after liming. The low apparent survival of the unselected hybrid group from Woods Lake in October 1985 appeared to be a sampling artifact, which we thought might be due to small fish not being captured effectively in our trapnets. However, comparisons of the size distributions of this group to that captured in the outlet trap which we believe had little size selectivity showed no difference ($t$-test, $p > 0.05$). Nevertheless, the abundance estimate for this group in spring 1986 was slightly higher than the previous fall and consistent with the abundance estimate for selected hybrids. By the fall of 1986, there was a significantly greater estimated abundance (nonoverlapping 95% confidence intervals) of the 1985 year-class selected group ($0+T\times D(s)$) in Woods Lake versus the unselected group ($0+T\times D$). This difference should be considered tentatively as other studies (Schofield et al. 1986) have failed to show consistent differences in survival between these groups.

The 1984 year-class (age 1+ at stocking) exhibited similar survival (48 versus 54%) in each lake from June to October of 1985. However, marked differences in survival between lakes occurred between fall 1985 and spring 1986, the period when Cranberry Pond reacidified (Driscoll et al. 1989). The abundance of fish in Cranberry Pond was so low in the spring of 1986 that we could not quantify it for any cohorts by mark-recapture techniques.

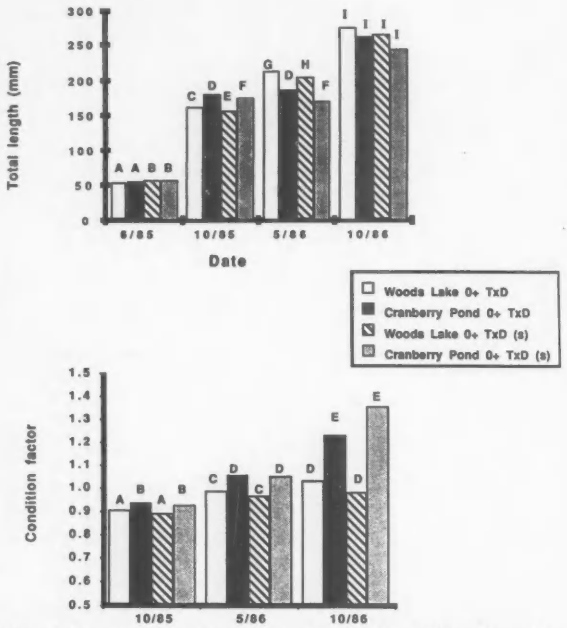


FIG. 4. Comparison of (a) total length and (b) condition factor for cohorts of brook trout stocked in Woods Lake and Cranberry Pond after liming in June 1985. Bars with the same letter are not statistically different, $p > 0.05$, ANOVA, Duncans NMRT.

Annual survival rates (corrected for fish removed for diet analysis) for the selected and unselected hybrids in Woods Lake were both 35% although confidence limits (C.L.) ranged from 20 to 67%. Annual survival for the 1984 year class Temiscamie strain was 21% (C.L. 16–30%) based on point estimates of population size. The survival estimated according to the Jolly–Seber method for the 1100 marked fish was 25% (C.L. 22–28%).

Emigration was important in both lakes as a source of population loss (Fig. 2 and 3). However, the pattern of emigration was very different between lakes in 1985 and between years for Woods Lake. The first significant emigration occurred in Woods Lake during October 1985 when over 160 of the 1-yr old Temiscamie fish ($1+T$) were captured in the outlet trap. This represented approximately 30% of the adult population present in October. These outmigrants were returned to the lake (see methods). Less than 10% of the outmigrants emigrated again after being returned. Emigration of the 1985 year class hybrids was insignificant during this period. In contrast, there was no emigration from Cranberry Pond during October. However, as the lake began to reacidify and pH dropped precipitously from 6.5 to 5.0 in November, there was rapid and large scale emigration of both the selected and unselected hybrids from Cranberry Pond. The emigration loss during this period was from 50–65% of the total estimated abundances for these two cohorts. The 1-yr old Temiscamie fish ($1+T$) outmigrated at a lower (25%) but substantial rate as well. Pulses of migration also occurred from Cranberry Pond again in response to the spring snowmelt in 1986. The number of outmigrants (~50 in each group of hybrids) exceeded those captured in the spring trapnetting. No additional migration occurred in the spring and the Cranberry Pond trap was not monitored after July 1986.

There was additional migration from Woods Lake in response to spring runoff for all cohorts, although the number emigrating was low and only sporadic emigration occurred during the summer of 1986. In contrast with the fall of 1985, there was virtually no migration from Woods Lake in the fall of 1986.

In Woods Lake, the 1985 year-class nonselected hybrids ($0+T\times D$) were smaller at stocking than the selected hybrids ($0+T\times D(s)$), but this difference did not persist and the $0+T\times D(s)$ fish were significantly longer than the $0+T\times D$ fish at each subsequent sampling (Fig. 4, ANOVA, $p < 0.05$). However, no difference in condition factor was evident at any time in Woods Lake. In Cranberry Pond a similar change in relative length occurred but was only significant at the second sampling. Condition factor did not differ between selected and unselected groups in Cranberry Pond. Within groups in each lake both length and condition factor increased significantly over time.

Condition factors and lengths differed between the two lakes but consistent patterns were not apparent. Initially, neither condition factor or length were different for selected hybrids since all fish were from the same stock. By October 1985 selected fish in Cranberry Pond were significantly longer than those in Woods Lake, but condition factors were not different. Condition factor became higher in Cranberry Pond by May 1986 while length had become greater in Woods Lake. Condition factors continued to be greater for the small number of fish in Cranberry Pond through October 1986 but no difference in length existed between the two lakes. Nonselected hybrids exhibited this same pattern with respect to length in the two lakes, while condition factors, again, were consistently greater in Cranberry Pond (ANOVA, $p < 0.05$).

The small amount of growth evident from comparing length at capture in the spring and back calculated lengths from spring scale samples (Table 2) suggested that annulus formation occurred at approximately the time of ice-out. Additionally, a high proportion of fish from spring trapnet samples exhibited incomplete annulus formation. Back calculated lengths also corroborated the actual length differences observed in trapnet samples between lakes and groups. Scale analysis further indicated a very high incidence of false annuli (~95%) for both groups of 1985 year class hybrid trout from both lakes. Back calculation of length at false annulus formation indicated that these were formed during the summer of 1985. During 1985, the 1-yr old Temiscamie strain ($1+T$) had a relatively low incidence of false annuli (<15%) in Woods Lake but 61% ($n=22$) had false annuli in Cranberry Pond.

## Natural Reproduction

Habitat surveys of substrate suitability and groundwater seepage in Woods Lake indicated that the quality of substrate and seepage water were suitable for brook trout spawning in several areas. Seepage water quality in May and November 1985 was not different with a range of pH 5.9–7.15, calcium 66–592 $meq\cdot L^{-1}$, and total aluminum was less than 0.8 $\mu mol\cdot L^{-1}$. Substrate was more sand than gravel. However, the rate of inflow of groundwater to the lake was quite low (Table 3). Carline (1980) reported seepage velocities of 11.5 to 45 $cm\cdot h^{-1}$ for spawning sites used by brook trout in Wisconsin lakes, whereas the highest velocity measured in Woods Lake was 2.56 $cm\cdot h^{-1}$ and occurred in June 1985. Velocities were less

TABLE 2. Comparison of mean total length (millimetres) of brook trout year-classes and strains in Woods Lake (*W*) and Cranberry Pond (*C*) after liming. Standard deviations are in parenthesis; number of sites measured (*n*).

| Year-class and strain | | Date[a] | | | | Age[b] | |
|---|---|---|---|---|---|---|---|
| | | 6/85 | 10/85 | 5/86 | 10/86 | I | II |
| 1985 $T \times D(s)$ | *W* | 57(4) | 157(19) | 205(25) | 265(23) | 199(21) | — |
| | *n* | 100 | 170 | 170 | 180 | 116 | |
| | *C* | 57(4) | 174(14) | 179(14) | 244(30) | 177(11) | — |
| | *n* | 100 | 135 | 6 | 2 | 24 | |
| 1985 $T \times D$ | *W* | 55(4) | 162(6) | 213(23) | 274(26) | 203(21) | — |
| | n | 100 | 212 | 216 | 109 | 156 | |
| | *C* | 55(4) | 180(12) | 186(14) | 261(20) | 178(15) | — |
| | *n* | 100 | 224 | 34 | 7 | 30 | |
| 1984 Temiscamie | *W* | 240(16) | 266(20) | 296(16) | 341(65) | 183(20) | 287(17) |
| | *n* | 1080 | 301 | 146 | 6 | 109 | 102 |
| | *C* | 240(16) | 284(15) | | | 192(21) | — |
| | *n* | 1080 | 168 | | | 36 | |

[a]Observed
[b]Calculated from 1986 samples.

TABLE 3. Seepage velocities along groundwater inflow transects in Woods Lake. (*n* = number of sites measured).

| | 1985 | | | | | | 1986 | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Date | 5/1–3 | 5/22–29 | 6/25–29 | 7/30–8/7 | 9/16–18 | 11/5–7 | 4/29–30 | 6/28–29 | 8/11–12 | 9/24–25 |
| Velocity $cm \cdot h^{-1}$ | 0.44 | 0.28 | 1.39 | 0.19 | 0.29 | 0.36 | 0.35 | 0.27 | 0.39 | 0.49 |
| Range | 0.19–1.00 | 0.01–0.50 | 0–2.56 | 0.02–0.51 | 0.02–1.79 | 0.02–1.71 | 0.03–2.17 | 0.00–2.03 | 0.00–1.75 | 0.00–1.94 |
| *n* | 8 | 16 | 28 | 35 | 33 | 41 | 41 | 42 | 44 | 44 |

TABLE 4. Comparison of the number of brook trout fry emerging from portions of spawning boxes in Woods Lake, Spring 1986.

| Box | 1* | 2* | 3* | 4 | Total* |
|---|---|---|---|---|---|
| Calcareous | 51 | 48 | 56 | 38 | 193 |
| Granitic | 17 | 26 | 31 | 42 | 116 |
| Total | 68 | 74 | 87 | 80 | 309 |

*Proportion emerging from substrates different at $p < 0.05$, Chi-square analysis.

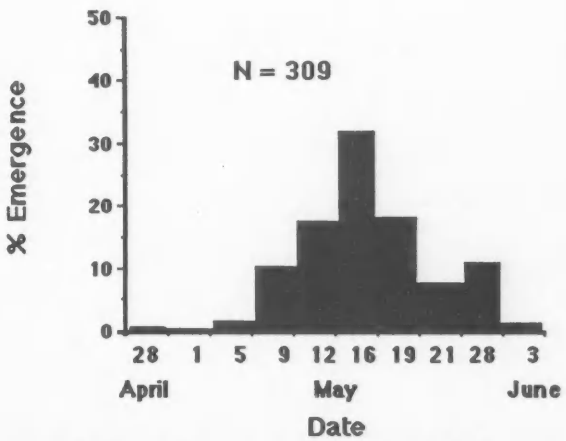


FIG. 5. Frequency distribution of brook trout fry captured in emergence traps placed over artificial spawning substrates in Woods Lake during spring 1986.

than 2.0 $cm \cdot h^{-1}$ during spawning and incubation periods. This finding led to the construction of spawning boxes to augment the potential for natural reproduction (Webster 1962).

Visual surveys of the littoral area in Woods Lake during October and November of 1985 resulted in the location of four natural redds in the low velocity seepage areas. Conversely, there was an extreme amount of spawning activity on the spawning boxes to the extent that individual redds were indistinguishable. Habitat surveys and visual observation for spawning activity in Cranberry Pond indicated no usable substrate or spawning activity.

Fry emergence began on April 28 in Woods Lake and continued until June 3, 1986 (Table 4, Fig. 5). No fry were captured from emergence traps on natural redds. Individual spawning boxes showed significantly more fry emerging from calcareous substrate in three of four cases, and a significant difference existed in overall emergence rate ($\chi^2$, $p < 0.05$). Extrapolation of the emergence rates from the area covered by traps in the boxes indicated that 700 fry emerged in 1986. Visual surveys in Woods Lake during the fall of 1986 resulted in location of 20–25 natural redds and less activity on the spawning boxes (9 redds).

## Food Utilization

The diet of age 1 + brook trout in Woods Lake and Cranberry Pond was comprised almost entirely of invertebrates, either insect larvae or microcrustaceans (Table 5 and 6). Few vertebrate prey organisms were observed. There was considerable variation in prey utilization from month to month in both lakes and between years for Woods Lake. No comparison between years could be made for Cranberry Pond. Although Cladocera

TABLE 5. Percent of total prey items by taxa for 1984 year-class brook trout introduced to Woods Lake and Cranberry Pond at age 1+, June 3, 1985. Percent frequency of occurrence in stomachs (in parenthesis), $n$ = number of stomachs examined, $P$ = mean number of prey items per stomach, $TL$ = mean total length of fish in millimetres, $W$ = Woods Lake, $C$ = Cranberry Pond. (1986 data are I+ 1985 year-class stocked as spring fingerlings in 1985).

| | 1985 | | | | | | 1986 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | June | July | Aug. | Sept. | Oct. | Nov. | April | May | June | July | Aug. | Sept. | Oct. |
| **Woods Lake** | | | | | | | | | | | | | |
| Anisoptera | 36(80) | 14(33) | 2(25) | 9(13) | 38(90) | 2(40) | 2(50) | <1(14) | 0(0) | 18(33) | 22(86) | 1(83) | 14(100) |
| Zygoptera | 18(65) | <1(11) | 67(83) | 11(88) | 24(73) | 2(40) | 31(100) | 1(29) | 1(25) | 49(33) | 15(43) | 10(83) | 37(100) |
| Tricoptera | 4(40) | 13(77) | 1(42) | 28(75) | 26(64) | 34(100) | 11(50) | 10(42) | 4(75) | 3(17) | 3(57) | <1(17) | 5(67) |
| Coleoptera | 10(55) | 0(0) | 3(33) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | <1(25) | <1(3) | 0(0) | 0(0) | 0(0) |
| Megaloptera | 2(30) | 1(22) | 1(25) | 0(0) | 1(9) | 2(60) | 0(0) | 4(43) | 0(38) | 0(0) | 0(0) | 0(0) | 2(100) |
| Hemiptera | 11(55) | 0(0) | <1(8) | 1(3) | 0(0) | 0(0) | 0(0) | 0(0) | 1(25) | 10(36) | 12(71) | 0(0) | 1(33) |
| Chironomidae | 1(5) | 1(33) | <1(75) | 38(88) | 6(27) | 1(20) | 0(0) | 43(100) | 49(63) | 16(33) | 42(100) | 30(83) | 9(67) |
| Chaoboridae | 0(0) | 1(11) | <1(17) | 7(25) | 0(0) | 0(0) | 0(0) | 30(86) | 45(38) | 1(6) | 0(0) | <1(17) | <1(33) |
| Ephemeroptera | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | 57(60) | 56(100) | <1(14) | 0(0) | 1(50) | 0(0) | <1(50) | 29(100) |
| Hydracarina | 17(15) | 68(22) | 19(50) | 2(25) | 1(9) | 1(20) | 0(0) | 12(71) | 0(0) | 0(0) | 5(29) | 59(83) | 1(67) |
| Amphipoda | 1(20) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) |
| Miscellaneous | 1(20) | 1(11) | 2(25) | 5(50) | <1(18) | 0(0) | 0(0) | <1(14) | 0(0) | 1(11) | 1(29) | 0(0) | 0(0) |
| $P$ | 24 | 23 | 104 | 19 | 7 | 25 | 23 | 31 | 93 | 9 | 30 | 266 | 53 |
| $n$ | 20 | 9 | 12 | 8 | 11 | 5 | 2 | 7 | 8 | 36 | 7 | 6 | 3 |
| $TL$ | 249 | 175 | 257 | 232 | 254 | 277 | 223 | 283 | 234 | 253 | 263 | 272 | 282 |
| **Cranberry Pond** | | | | | | | | | | | | | |
| Anisoptera | 2(100) | 9(73) | 0(0) | 23(76) | 36(77) | 37(80) | | | | | | | |
| Zygoptera | <1(33) | 1(9) | 15(50) | 7(53) | 21(44) | 2(20) | | | | | | | |
| Tricoptera | 1(50) | 26(100) | 0(0) | 4(35) | 32(44) | 2(20) | | | | | | | |
| Coleoptera | <1(17) | 0(0) | 0(0) | 0(0) | 0(0) | 4(20) | | | | | | | |
| Megaloptera | 0(0) | 1(18) | 0(0) | 0(0) | 0(0) | 0(0) | | | | | | | |
| Hemiptera | 2(83) | 0(0) | 0(0) | 2(24) | 7(33) | 7(40) | | | | | | | |
| Chironomidae | 1(67) | 48(82) | 83(100) | 57(65) | 0(0) | 0(0) | | | | | | | |
| Chaoboridae | 94(67) | 16(27) | 1(38) | 5(29) | 0(0) | 2(20) | | | | | | | |
| Ephemeroptera | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | 7(40) | | | | | | | |
| Hydracarina | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) | | | | | | | |
| Amphipoda | 0(0) | 0(0) | 0(0) | 1(18) | 4(22) | 14(40) | | | | | | | |
| Miscellaneous | 0(0) | <1(9) | 0(0) | <1(18) | 0(0) | 26(40) | | | | | | | |
| $P$ | 275 | 21 | 59 | 21 | 6 | 11 | | | | | | | |
| $n$ | 6 | 11 | 8 | 17 | 9 | 5 | | | | | | | |
| $TL$ | 259 | 255 | 218 | 264 | 242 | 254 | | | | | | | |

TABLE 6. Major invertebrate prey taxa utilized by brook trout in Woods Lake and Cranberry Pond.

| | Woods Lake | | Cranberry Pond |
|---|---|---|---|
| Taxon | 1985 | 1986 | 1985 |
| Anisoptera | *Leucorrhinia*<br>*Ladona* | *Boyeria*<br>*Cordulia* | *Leucorrhinia*, *Ladona*<br>*Cordulia*, *Boyeria* |
| Zygoptera | *Enallagama* | *Enallagama* | *Enallagama* |
| Trichoptera | *Phryganeidae*<br>*Polycentropodidae* | *Phryganeidae*<br>*Polycentropodidae* | *Phryganeidae*<br>*Polycentropodidae* |
| Coleoptera | *Gyrinus*, *Dineutus* | — | — |
| Megaloptera | — | *Sailis* | — |
| Diptera | *Chironomidae* | *Chironomidae*<br>*Chironomidae* | *Chaoborus* |
| Hemiptera | *Notonecta* | *Hesperocoria* | *Hesperocoria* |
| Hydracarina | unknown | unknown | — |
| Cladocera | *Eurycercus*<br>*Daphnia catawba* | *Daphnia catawba* | *Sida crystallina*<br>*Daphnia catawba* |

and Diptera were often numerically important, Anisoptera in Woods Lake and Cranberry Pond and Zygoptera in Woods Lake were more important energy sources (Fig. 6 and 7). Cladocera became important in terms of caloric value in the fall in both lakes during 1985 and were consistently important in Woods Lake during 1986.

## Discussion

Cranberry Pond and Woods Lake have provided some of the first quantitative information relative to the introduction of brook trout populations in previously acidic waters. Schofield et al. (1986) have reported brook trout data from the study of

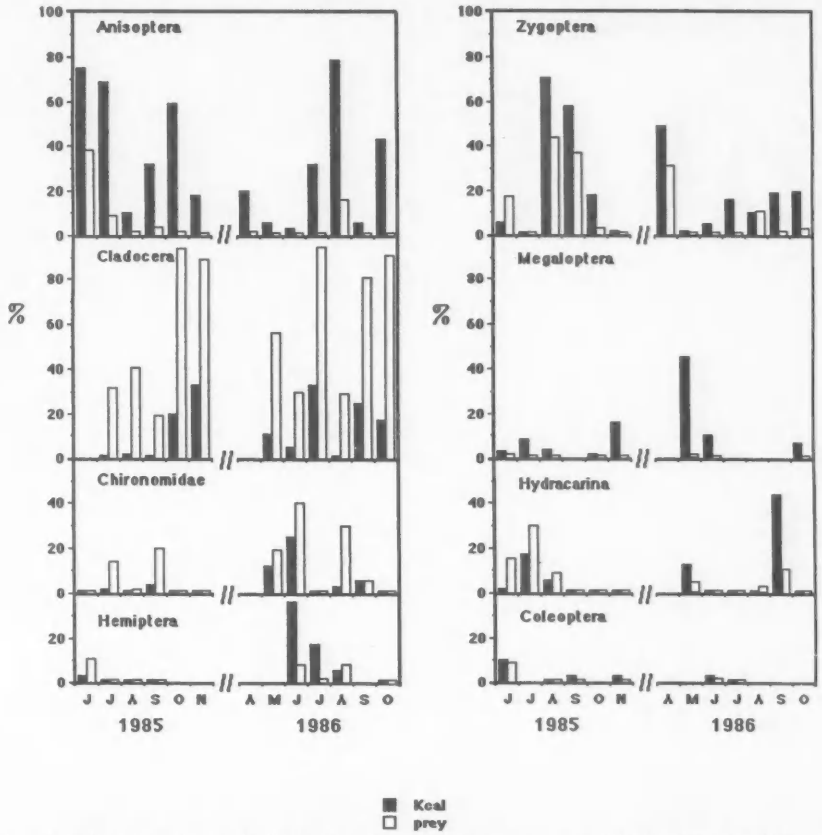


FIG. 6. Relative numbers and caloric values for major prey taxa consumed by brook trout >200 mm in Woods Lake during open water periods in 1985–86.

10 small Adirondack lakes neutralized with agricultural limestone in 1983 and 1984. However, the principal sources of data for comparison with the populations we have studied comes from data on brook trout in nonacidified lakes in the eastern United States and Canada. Survival estimates for the spring fingerling fish over the first 4 mo after stocking in both lakes were nearly identical (66 versus 64%) to average survival rates for these and other strains reported for circumneutral Adirondack lakes by Webster and Flick (1981). This calculation does not include the apparently errant but low (35%) estimated survival for the unselected ($0+T\times D$) group in Woods Lake. The survival rates in Woods Lake are lower after 1 yr, averaging 35%, than estimates of first year survival of fall planted fingerlings in 10 lakes during the first year after liming (range 60–80%) reported by Schofield et al. (1986). However, fish stocked as fall fingerlings should probably exhibit less mortality than when the same strain is stocked earlier. Nevertheless, the age 1+ fish stocked in Woods Lake also exhibited relatively low annual survival (21% by Schnabel, 25% by Jolly–Seber). Estimated annual survival rates for Assinica strain and hybrid Assinica × domestic brook trout stocked in six Michigan lakes as fall fingerlings ranged from 33 to 86% but averaged 63% (Gowing 1986).

Survival and longevity as well as production of brook trout in Adirondack waters are generally lower than in other geographic areas (Webster and Flick 1981; Fraser 1981; Gowing 1986; Schofield et al. 1989). It is likely that early summer stocking combined with some incomplete chemical mixing in Woods Lake (Driscoll et al. 1989) may have contributed to lower survival than fall stocked fish in similarly limed waters in the Adirondacks (Schofield et al. 1986). There are additional indications based upon the occurrence of false annuli on scales during summer and the proportion of annual growth occurring over winter (Schofield et al. 1989) that summer conditions in these two lakes may not be optimal for brook trout. Hatch (1961) hypothesized that temperatures in relatively shallow Adirondack lakes reached levels that interrupted brook trout growth and resulted in a high frequency of false annuli. However, overall growth and production were similar to other Adirondack waters (Schofield et al. 1989).

The apparent improved survival of the acid tolerant hybrid in Woods Lake in October 1986 should be interpreted cautiously. Schofield et al. (1986) found only occasional differences in survival for these groups of fish in 10 limed lakes in the Adirondacks and those differences were not consistent.

Behavioral influences on observed or potential population losses in these limed lakes were important. For example, in Woods Lake approximately 30% of the estimated number of age 1+ fish emigrated from the lake during October of 1985, the first fall after stocking. While these fish were captured in the outlet trap and returned to the lake, in a typical lake with a downstream impassable falls near the outlet these fish would

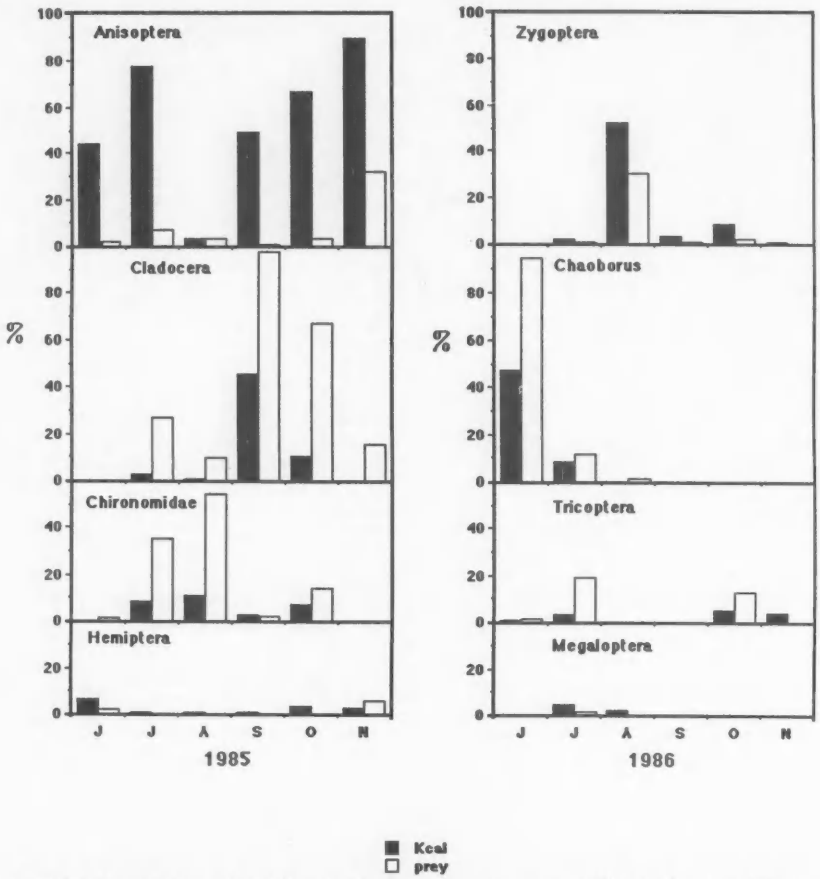


FIG. 7. Relative numbers and caloric values for major prey taxa consumed by brook trout >200 mm in Cranberry Pond during open water period 1985.

have been lost and treated as additional mortality. This behavior coincided with the spawning period and may have been exacerbated by the relative paucity of suitable groundwater seepage areas in the lake. However, in 1986 the reproductively mature fish behaved differently with virtually no emigration occurring in this population which had spent 15–16 mo in the lake (Fig. 2). Similarly the importance of behavioral factors in accounting for population losses during rapid reacidification of limed lakes was obvious in Cranberry Pond where the majority of the population emigrated rather than remain in a physiologically stressful situation (Fig. 3). This contrasts with the behavior of fish stocked into Woods Lake prior to liming when in-lake mortality rather than emigration accounted for most of the population loss over winter (Gloss et al. 1987).

Length attained at the various sampling periods (Table 2) was similar to that of stocked fish in other Adirondack lakes, both limed and circumneutral (Schofield et al. 1986; Flick and Webster 1976) and to the length of similar age brook trout stocked in Michigan lakes (Gowing 1986). However, similar age brook trout in Ontario lakes were substantially longer than fish in Woods Lake and Cranberry Pond (Fraser 1981, 1983).

Natural reproduction has been observed only in Woods Lake and only from redds constructed on the artificial spawning boxes. The level of reproduction has not been sufficient to sustain a brook trout population in Woods Lake. Although more redd construction occurred on natural substrates in the fall of 1986, there was no emergence of fry and only two fry were captured in emergence traps on the spawning boxes in 1987 (R. Spateholts, unpubl. data). Brook trout typically select spawning areas with ample upwelling water, and this has been suggested as being more important than substrate composition (Webster 1962; Webster and Eriksdotter 1976; Fraser 1985). Fraser (1985) and Webster (1962) suggested that population size in some lakes may be limited by the availability of suitable spawning sites. This clearly appears to be the case in Woods Lake. Moreover, brook trout typically spawn in streams and rivers, rather than lakes. Two tributary streams to Woods Lake appear to have suitable flow and substrate conditions for brook trout spawning. However, the water quality conditions, primarily acidity and aluminum, are such that fish cannot survive. It is possible that reduction in acid loadings to these streams might result in an alternative reproductive strategy by the brook trout population in Woods Lake whereby tributary spawning could sustain the lake population. This strategy has been suggested by Power (1980).

Peak emergence in Woods Lake occurred in mid-May 1986. This was approximately 5 wk after the ice melted on Woods Lake and 6–7 wk past the peak spring runoff, the time when

the most extreme chemical conditions in surface and nearshore waters usually occur. This suggests that population loss of brook trout from lakes in the Adirondacks may be due to long-term acidification effects rather than acute toxicity to early life stages. Such a mechanism of population failure was suggested by Frenette and Dodson (1984) for an acidifying Quebec lake. However, Fraser (1985) reported emergence of brook trout fry in March and April in an Ontario lake where intragravel water temperatures ranged from 1.1 to 4.4°C during January through March and emergence coincided with the spring melt pH depression (pH 5.1). Further study of the fry emergence period in Adirondack waters is warranted. It is possible that the tributary inflow water supply to the spawning boxes was considerably cooler than natural groundwater seepage flows and may have slowed embryonic development, thereby retarding hatch and emergence until later than natural redds.

Our diet analysis, which should be regarded as semiquantitative, provides further documentation of the opportunistic feeding by brook trout. The immediate effect of the brook trout introduction in Cranberry Pond was the virtual elimination of *Chaoborus americanus* which was the numerically dominant water column macroinvertebrate prior to liming. The prevalence of these organisms in brook trout stomachs during June 1985 provides strong circumstantial evidence that their elimination was due to predation (Evans 1989; Schaffner 1989). The increased importance of zooplankton in the diet of Woods Lake fish also suggests that larger prey items may have become less abundant. Evans (1989) documented dramatic reductions in the populations of water column macroinvertebrates following fish introductions to both Woods Lake and Cranberry Pond. Nilsson (1972) discussed similar changes in the invertebrate fauna of barren lakes after fish were introduced. Very little was known about the long-term stability of prey communities in acidic lakes following initial liming and subsequent fish stocking. According to Powers (1980), insights into the fundamental ecology of energy flux in brook trout populations were lacking. Schofield et al. (1989) discuss the importance of changes in food resources on production and growth efficiency of brook trout in Woods Lake and Cranberry Pond.

Under current acidic deposition regimes in the Adirondack region of New York, reacidification of limed lakes is dependent primarily on retention time. Our data demonstrate the reintroduction and restoration of brook trout populations in these lakes is feasible (at least initially) so long as suitable water quality conditions are maintained. The response of brook trout after liming should be similar to what we might expect if water quality were improved more gradually (e.g. by reduction of acidic inputs). The long-term stability of food resources and potential for establishing naturally reproducing populations in lakes of this region require further study.

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# Effects of Liming on the Epipelic Algal Community of Woods Lake, New York[1]

Deborah A. Roberts and Charles W. Boylen[2]

*Department of Biology and Fresh Water Institute, Rensselaer Polytechnic Institute, Troy, NY 12180-3590, USA*

Roberts, D. A., and C. W. Boylen. 1989. Effects of liming on the epipelic algal community of Woods Lake, New York. Can. J. Fish. Aquat. Sci. 46: 287–294.

The biovolume and species composition of algae on the sediment along a depth gradient were determined before and after liming of acidic (pH 4.9), oligotrophic Woods Lake in the Adirondack Park in New York State (Herkimer Co., NY, USA). The epipelic algal community was dominated by diatoms and cyanobacteria prior to and following liming. Distinct depth zonation patterns of community composition were evident and unaffected by $CaCO_3$ addition. Treatment with calcite increased pH from 4.9 to above 9.0, caused ANC to rise from 0 to >400 $\mu eq \cdot L^{-1}$, and immediately reduced overall water clarity which subsequently improved during the summer. There was a significant decrease ($p < 0.001$) in total algal biovolume after liming corresponding to a significant reduction in biovolume of *Hapalosiphon pumilus* at the deepest sites. Total diatom biovolume was not significantly changed as a result of the addition of calcite; however, a shift in community composition from dominance by *Navicula tenuicephala* and *Fragilaria acidobiontica* to dominance by *Achnanthes microcephala* and *Anomoeoneis vitrea* was observed following liming.

On a déterminé, suivant un gradient de profondeur, le biovolume et la composition en espèces des populations algales des sédiments avant et après un traitement de neutralisation; cette étude portait sur le lac Woods, nappe d'eau oligotrophe acidifiée (pH : 4,9) des Adirondacks dans l'État de New York (Herkimer Co., NY, USA). Les diatomées et les cyanobactéries prédominaient dans la communauté d'algues épipélagique avant et après la neutralisation. La composition de la communauté suivait à l'évidence une zonation par profondeurs bien établie qui n'a pas été modifiée par l'application de $CaCO_3$. Par suite du traitement à la calcite, le pH a augmenté, passant de 4,9 à plus 9,0, la CNA est passée de 0 à plus de 400 $\mu eq \cdot L^{-1}$ et, dans l'ensemble, la transparence des eaux a diminué immédiatement après le traitement, puis elle s'est améliorée au cours de l'été. Le biovolume algal total a diminué dans une mesure significative (p inf. à 0,001) après le traitement : cette diminution correspond à une baisse significative du biovolume de *Hapalosiphon pumilus* dans les parties les plus profondes. Le biovolume total des diatomées n'a pas été modifié de façon significative par le traitement à la calcite; la composition de la communauté a cependant changé : *Navicula tenuicephala* et *Fragilaria acidobiontica*, espèces auparavant les plus abondantes, ont été supplantées par *Achnanthes microcephala* et *Anomoeoneis vitrea* après la neutralisation.

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One commonly reported effect of acidification on aquatic ecosystems is an alteration in the biomass and structure of attached algal communities including the development of benthic mats of blue-green algae (cyanobacteria) or clouds of filamentous green algae in shallow water (Lazarek 1980; Stokes 1981, 1986; Turner et al. 1987). The development of mats of cyanobacteria has not been definitively correlated to acidification and factors regulating this phenomenon are still undefined (Stevenson et al. 1985; Turner et al. 1987; Roberts and Boylen 1988). Several hypotheses have been proposed by Stokes (1986) to explain the development of attached algal communities following acidification, including: the pH preference of algae; changes in grazing pressure; changes in microbial decomposition rates; and decreased competition with other algae.

An objective of the present study was to further address these various hypotheses by documenting the effects of elevating the pH in a whole lake manipulation experiment. The hypothesis that a particular community, such as epipelic algae, is favored by the chemical conditions in acidic lakes can be tested in a whole lake liming experiment. Simply establishing the pH preference of a particular species will not adequately address this question, since field distributions are determined not only by individual species preferences, but also by resource partitioning and species competition.

A manipulation such as liming will influence a complex of physical, chemical, and biological factors, making it difficult to interpret the underlying mechanisms influencing the response of individual species. However, the nature and time scale of the community response may provide strong indications about probable mechanisms. An increase or decrease in total standing crop would be expected if the availability of an important resource was altered. A change in benthic invertebrate grazing

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[2]Author to whom correspondence should be addressed.

pressure is unlikely to occur for months or even over an entire growing season because of the length of the life cycles of invertebrates. In contrast, direct responses of epipelic algae to changes in water chemistry would be expected to occur on a much shorter time scale.

The experimental neutralization of Woods Lake (Herkimer Co., NY, USA) provided the opportunity to evaluate the response of the epipelic algae in a system with a known, long-term chemical history as well as a pH history reconstructed from paleolimnological investigation of diatom remains. Woods Lake was limed (addition of $CaCO_3$ to the surface water) in May 1985 as part of the Lake Acidification Mitigation Project (LAMP) (Porcella 1989). The depth distribution and seasonal variation of the epipelic algal communities in this Adirondack lake were characterized, in detail, one year prior to liming (Roberts and Boylen 1988). The presence of both a cyanobacterial mat in deep water and a diverse diatom community in shallow water made it a valuable site for a neutralization experiment since the response of both types of associations could be determined. The objectives of the benthic algal community studies in conjunction with the liming experiment were to investigate the effects of chemical neutralization on: seasonal patterns and depth distribution of total standing crop; community composition; and the abundance of individual species. A paleolimnological diatom record of Woods Lake (Davis et al. 1986) was extremely valuable for interpreting changes in diatom communities induced by liming. Since the study spanned only one growing season before and one after liming, the natural seasonal fluctuations in biomass of nondiatom taxa could not be separated entirely from the effects of liming.

## Methods

### Physical/Chemical Measurements

A detailed characterization of the variation in water chemistry of Woods Lake prior to and following liming was reported by Fordham and Driscoll (1989) and Driscoll et al. (1989a, b). A subset of these data obtained from samples collected mid-lake, monthly from May through August and in October during 1984 and 1985 was used to characterize the chemical environment of this lake's epipelic algal community. Sampling to supply chemical data occurred up to several days before or after algal collections. To verify that these data were representative of the conditions at the time and site of the algal collections, additional lake water samples were obtained at algal collection sites (just above the sediments). These water samples were analyzed for pH and acid neutralizing capacity (ANC) using methods consistent with those used by Fordham and Driscoll (1989).

Light and temperature profiles were also measured at the mid-lake site monthly, May through August, and in October 1985 on the dates of the algal collections. Light profiles were measured at 1 m intervals using a Licor Lambda (LI 185) submersible photometer. Temperature profiles were measured at 1 m intervals with a YSI model 57 field meter.

### Collections and Processing of Algal Samples

Epipelic algal samples were collected monthly from May to August and in October during 1984 and 1985. Three depths along a single transect perpendicular to the shoreline were sampled (1, 4, and 7 m). At each depth, nine replicate intact cores (35 mm diameter) were collected by hand using SCUBA. The top 1.5 cm of each of three cores was pooled to form three replicate pooled samples from each depth (with the exception of May 1984, when nine individual cores were analyzed for each depth). The algae were preserved and direct counts of cells with intact protoplasm were made using the methods described in Roberts and Boylen (1988). Raw counts were converted to biovolume data by calculating a cell volume for each form identified (Roberts and Boylen 1988).

### Statistical Analyses

A three-way analysis of variance (ANOVA) and Tukey, pairwise comparisons were used to identify differences in total biovolume for various taxa with respect to depths, sampling dates and the two years of the study. May 1985 samples were collected prior to the calcite addition. Consequently, all analyses between years to examine differences before and after liming were done with June through October samples only. Log-transformed biovolumes were used for the ANOVA procedures. Exact probabilities for the significance of the $F$ statistic are reported. For posthoc comparisons the threshold for the level of significance was chosen to be $p < 0.05$.

Pearson correlation coefficients were calculated between the average log-transformed biovolumes of 16 selected taxa and all of measured chemistry variables (see Table 1 for listing). The taxa included total algae, Cyanobacteria, Chlorophyceae, Bacillariophyceae, *Anacystis* spp., *Hapalosiphon pumilus* (Kutz.) Kirchner, *Eunotia* spp., *Melosira* spp., *Pinnularia* spp., *Achnanthes microcephala* (Kutz.), *Anomoeoneis vitrea* (Grun.) Ross, *Cymbella microcephala* Grun., *Fragilaria acidobiontica* Charles, *Navicula subtilissima* Cl., and *N. tenuicephala* Hust. The 11 species or genera represented the three divisions present with eight being most common (present in > 50% of the samples) prior to liming and three which achieved high abundances after liming (> 100 cells·mm$^{-2}$). In addition, partial correlation coefficients were analyzed to determine how algal biovolume was related to water chemistry changes resulting from liming, after accounting for variation due to other habitat conditions. All statistical analyses were done using SPSS$^x$ (SPSS 1983; Norusis 1985) on the IBM 3081D computer at Rensselaer Polytechnic Institute.

## Results

### Water Chemistry

During the summer prior to liming, the pH of the epilimnetic water of Woods Lake ranged from 4.8 to 5.2 and the average ANC of the surface water was $-3$ μeq·L$^{-1}$. The chemical response of the lake water to the $CaCO_3$ is reported in detail by Fordham and Driscoll (1989) and Driscoll et al. (1989a, b). The calcite addition on May 30–31, 1985 increased the pH above 9.0 and the ANC above 400 μeq·L$^{-1}$. The trends in ANC and pH just above the sediments at 1, 4, and 7 m found during algal collections (Roberts 1987) were indistinguishable from data collected by Fordham and Driscoll (1989) at the open water site. The immediate effects of liming also included an increase in calcium, magnesium, dissolved inorganic carbon (DIC), and total fluoride concentrations and a decrease in aluminum, zinc, and manganese concentrations (Fordham and Driscoll 1989; Driscoll et al. 1989b).

The addition of calcite to Woods Lake dramatically reduced light penetration for several weeks after $CaCO_3$ addition. The transmittance was decreased from 71 to 43% at 1 m and from 7 to <1% at 7 m between the May 21, 1985 and June 5, 1985

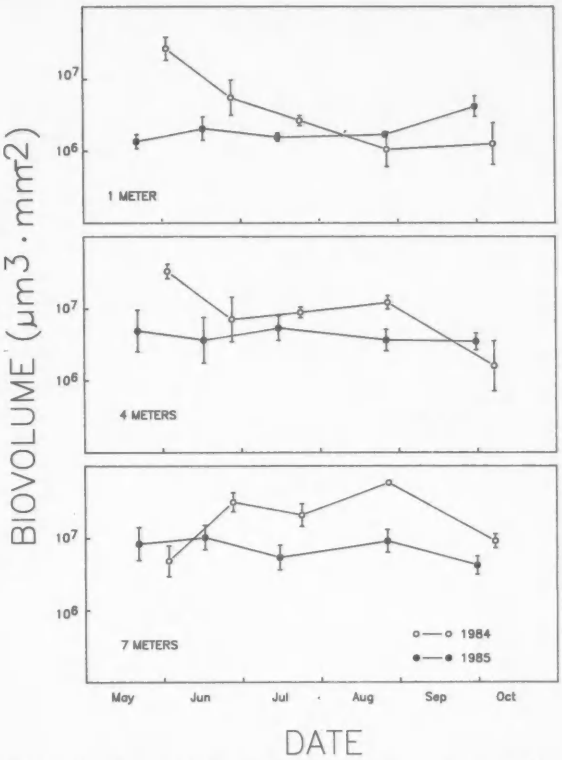


FIG. 1. Variation in total epipelic algal biovolume at 1, 4, and 7-m depths in Woods Lake, May through October during 1984 and 1985. Vertical bars represent one standard error ($n = 3$). The arrow indicates the date of the calcite addition.

measurements. Subsequently water transparency increased to values near that of the previous season (Bukaveckas 1989).

## Effects of Liming on Epipelic Algae

Total epipelic algal biovolume decreased significantly between 1984 and 1985 (ANOVA, $p = 0.001$). The effect between years was not the same at each depth sampled (Fig. 1). There was a significant (ANOVA, $p < 0.05$, Tukey allowances) decrease in total algal biovolume at the 7-m depth, but not at the 1-m or 4-m sampling sites. Total biovolumes were similar between depths in 1985 ($p > 0.05$), whereas in 1984, biovolume at 7 m was greater than at the other two depths ($p < 0.05$).

Diatoms and cyanobacteria continued to be the dominant components of the epipelic biovolume after the calcite treatment in 1985 (Fig. 2). Diatoms contributed the largest proportion of the biovolume at the 1- and 4-m depths during both the preliming and the postliming growing seasons. Cyanobacteria continued to be greater than 80% of the total biomass at the 7-m site in 1985.

The reduction in total biovolume at 7 m can be attributed to a significant decrease in cyanobacteria at that depth. Total biovolume of cyanobacteria over all of the sites ($p < 0.001$), and at both the 4 and 7-m sites ($p < 0.05$), was reduced in 1985. The decrease at 7 m was due to a decrease in the dominant species, *H. pumilus* (Kutz.) Kirchner. This branched, filamentous, cyanobacterium, which covered the sediments in 1984, did not attain nearly the same biomass as the previous season. *Hapalosiphon pumilus* biovolume was reduced at both 1 and 7-m depths between 1984 and 1985 ($p < 0.05$, Tukey allowances). Although the preliming biomass of this species was not significantly different from that of the May samples from the previous year, the biovolume of *H. pumilus* did not increase to produce a late summer maximum as it did in the preliming season.

Among the other cyanobacteria, *Anacystis* spp., the dominant genus of coccoid cyanobacteria, was also reduced ($p = 0.021$) in total biovolume between the 2 yr of the study. The biovolume of the Oscillatoriaceae, which was more abundant at the 1 and 4-m sites throughout both years of the study, was unchanged by the calcite addition ($p = 0.98$). *Schizothrix calcicola* (Ag.) Gomont was the dominant species in this group and also showed no significant response to the liming manipulation.

In contrast with the cyanobacteria, the total biovolume of the diatoms was unchanged after liming ($p = 0.12$). Many of the dominant species, however, did show significant changes in total biovolume in response to the calcite treatment. The total biovolume of two of the most abundant species in 1985, *N. tenuicephala* Hust. and *N. subtilissima* Cl., was lower ($p < 0.001$) than in the previous year. The reduction in *N. tenuicephala* biovolume was significant at both 1 and 4-m, the depths at which this species continued to be most abundant.

Another major component of the total diatom biovolume in 1984 at the shallower depths was *F. acidobiontica*. Charles. The relative abundance of this species was much lower at 1 m in 1985 than in the preliming season, but this was not significant (ANOVA, $p = 0.057$). Although the magnitude of the decrease in biovolume between years was similar to that of the two *Navicula* species, the error of measurement was much greater for *F. acidobiontica*, probably because it is a colonial form. There was also no significant effect of liming on *Eunotia* spp. or *Pinnularia* spp. biovolumes ($p > 0.20$).

Three new species of diatoms (*A. microcephala* Kutz.; *A. vitrea* (Gurn.) Ross; and *C. microcephala* Grun) appeared after liming in 1985. With the exception of a lower relative abundance of *F. acidobiontica*, the composition of the diatom community in early summer of 1985 was similar to the composition during the year prior to liming at both the 1 and 4-m depths (Fig. 3). The species composition at both of these depths changed dramatically between June and July of 1985. At 1 m there was a sharp drop in the relative abundance of *N. tenuicephala* and a concomitant increase in *C. microcephala*, and *A. microcephala*. By late August, *A. vitrea* had become dominant, and the numbers of *C. microcephala* had become substantially reduced at this depth (Fig. 3). At 4 m, *C. microcephala* never achieved the relative abundance observed during July and August at the 1-m site. However, a large increase in *A. microcephala* and *A. vitrea* during August was observed at the 4-m site. Similar to the 1-m site, there was also a sharp decrease in *N. tenuicephala* abundance by July at the 4-m site.

The diatom community at 7 m was not only a much smaller part of the total biovolume (Fig. 2), but also had a much different species composition throughout both sampling seasons than at the other two depths. The relative abundance of *N. tenuicephala* at 7 m was much lower than the other depths even in 1984 (Fig. 3), and contributed very little to the total diatom abundance after liming in 1985. *Eunotia* was one of the most common diatom taxa at 7 m in 1984. The most abundant species

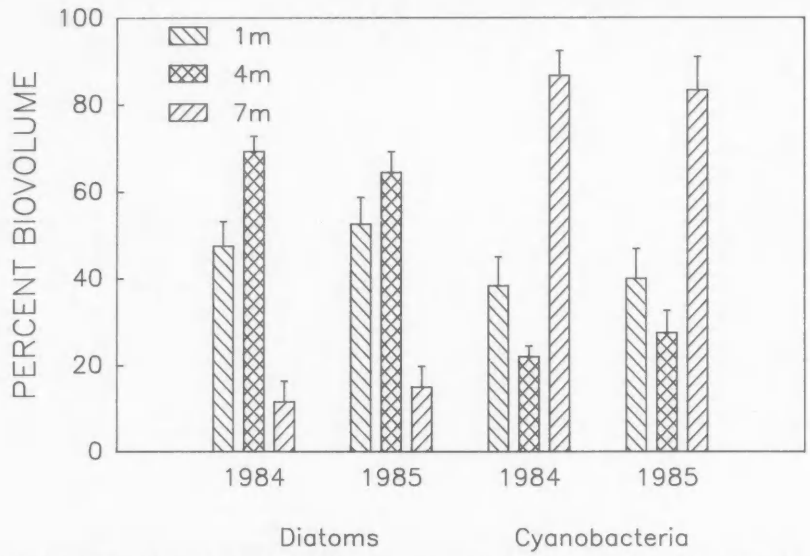


FIG. 2. Percent of the total epipelic algal biovolume represented by diatoms and cyanobacteria at three depths in Woods Lake, May through October during 1984 and June through October during 1985. Vertical bars represent one standard error.

was *E. curvata* (Kutz.) Lagerst. and was the dominant diatom species at 7 m throughout 1985.

Simple correlations of algal biovolumes with habitat variables showed that in addition to *H. pumilus* and *Eunotia* spp., total algal biovolume and cyanobacterial biovolume increased with depth (Table 1). A number of other taxa were negatively correlated ($p < 0.05$) with depth or depth squared. These included: Oscillatoriaceae, *Pinnularia* spp., *N. tenuicephala*, and *N. subtilissima*. Each of these had a higher correlation with depth squared (with the exception of *Pinnularia* spp. and total algal biovolume) than with depth. This indicates that increases or decreases with depth were more curvilinear than linear.

The biovolumes of *A. microcephala, A. vitrea, C. microcephala*, and *N. tenuicephala* all had significant correlations with pH or ANC, as well as several of the other variables associated with liming (Table 1). All of these species with the exception of *N. tenuicephala* increased in abundance after liming in 1985. The biovolumes of *A. microcephala, A. vitrea,* and *C. microcephala* also had positive correlations with dissolved organic carbon (DOC), DIC, calcium, and magnesium concentrations and negative correlations with manganese and zinc concentrations (Table 1).

In contrast with the weak correlations of biovolumes with most of the chemical variables when simple correlations were considered, several species had significant partial correlation coefficients with chemical variables when the variation in biovolumes due to depth was removed. When depth squared was accounted for, a decrease in total algal biovolume was significantly ($p < 0.05$) correlated with ANC, DIC, calcium, magnesium, zinc, and manganese concentrations, while total biovolume of diatoms and the biovolume of *F. acidobiontica* were positively correlated ($p < 0.05$) with organic aluminum concentration and negatively correlated with magnesium levels. Decreases in *H. pumilus* and *Eunotia* spp. were also correlated with liming variables (e.g. magnesium, zinc) when the effects of depth squared were removed. The biovolume of the Chlorophyceae was not significantly ($p > 0.05$) correlated to any of the habitat variables tested.

## Discussion

The changes in the epipelic algal communities within the first season postliming included a depth-dependent decrease in total biomass and dramatic changes in community composition, particularly among the diatoms. Differences in biomass between 1984 and 1985, particularly among the nondiatom taxa, must be interpreted with some caution since it is not known how much of the variation can be attributed to seasonal differences or to liming effects. The temperature increased more rapidly in the shallow water of Woods Lake in 1985 (Driscoll et al. 1989); however, total biomass in May was higher in 1984 compared with 1985 at both 1 and 4 m.

A large change in the community composition of diatoms occurred between the June and July samples of 1985. There was also an increase in the total compositional distance between these sampling dates measured as Euclidean distance between consecutive date pairs (Roberts 1987). This analysis indicated a lag in the population response of the epipelic algae to liming on the order of 6 – 7 wk.

Essentially the same community composition and species distributions with depth were observed in Woods Lake in May 1985, prior to liming, as were described in 1984. The only notable difference was a lower abundance of *F. acidobiontica* in the May 1985 samples. This is probably due to either differences in seasonal conditions or the sampling date in 1985 not corresponding with the peak distribution of this species.

A large portion of the total variation in algal biovolumes was explained by depth distribution. Biovolume of all but two of the common taxa decreased with depth; distributions were similar to those described by Roberts and Boylen (1988). The biovolume of *Eunotia* spp. and *H. pumilus* both indicated adaptation to low light conditions and had a positive correlation with

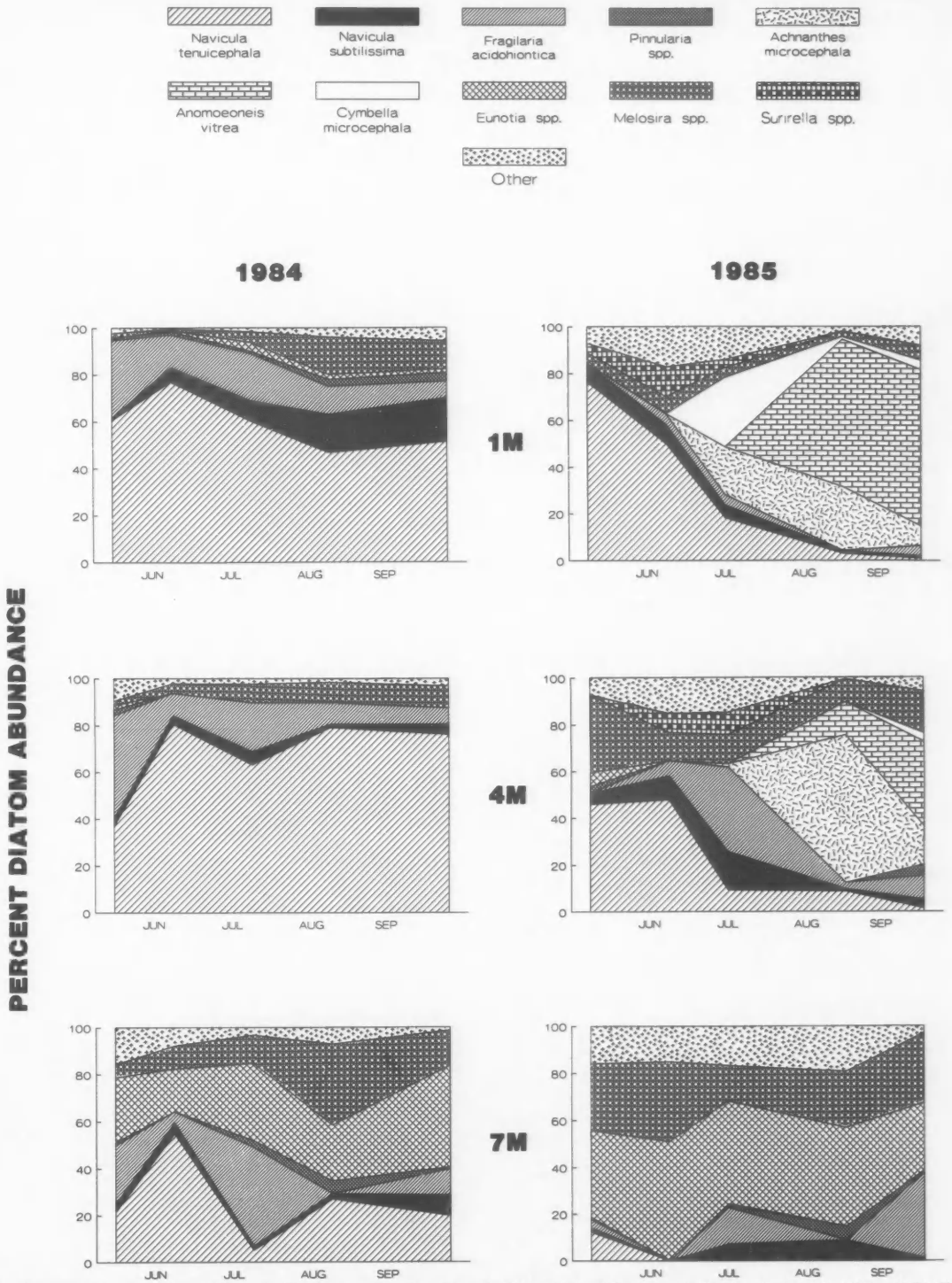


FIG. 3. Community composition of the epipelic diatoms at 1, 4, and 7 m in Woods Lake, May through October during (A) 1984 and (B) 1985. The percent of the total diatom abundance of each taxon is plotted for each sampling date.

TABLE 1. Pearson correlation coefficients (simple) between the log-transformed biovolumes of selected taxa and the chemical and physical variables. Several chemistry variables not included in the table had no significant ($p > 0.05$) correlation with any of the algal taxa. These included $Cl^-$, $NO_3^-$, $K^+$, Total Al, monomeric Al, and dissolved silica. Depth² = depth squared, ANC = acid neutralizing capacity, DOC = dissolved organic carbon, DIC = dissolved inorganic carbon, Al(ORG) = organic aluminum, TURB = turbidity, Light = percent light transmittance, TP = total phosphorus, TEMP = temperature, all other chemistry variables are as total concentration of the metal or ion. TOT = Total Algae, CHL = Chlorophyaceae, CYA = Cyanobacteria, OSC = Oscillatoriaceae, AAS = *Anacystis* spp., HAP = *Hapalosiphon pumilus*, DIA = Bacillariophyceae (diatoms), EUS = *Eunotia* spp., MES = *Melosira* spp., PIS = *Pinnularia* spp., ACM = *Achnanthes microcephala*, ANV = *Anomoeoneis vitrea*, CBM = *Cymbella microcephala*, FRA = *Fragilaria acidobiontica*, NAS = *Navicula subtilissima*, NAT = *Navicula tenvicephala*.

| Variable | TOT | CHL | CYA | OSC | AAS | HAP | DIA | EUS | MES | PIS | ACM | ANV | CBM | FRA | NAS | NAT |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Depth | 0.56[b] | −0.12 | 0.66[c] | −0.54[b] | −0.25 | 0.67[c] | −0.12 | 0.73[c] | −0.13 | 0.34[a] | −0.31 | −0.28 | −0.26 | −0.21 | −0.57[b] | −0.43[a] |
| Depth² | 0.54[b] | −0.08 | 0.71[c] | −0.63[c] | −0.31 | 0.76[c] | −0.23 | 0.78[c] | −0.21 | −0.30 | −0.34 | −0.30 | −0.26 | −0.26 | −0.62[c] | −0.50[b] |
| pH | −0.33 | 0.04 | −0.22 | −0.04 | −0.12 | −0.25 | −0.22 | −0.21 | −0.13 | −0.02 | 0.58[c] | 0.48[b] | 0.47[b] | −0.24 | −0.29 | −0.59[c] |
| ANC | −0.30 | 0.02 | −0.23 | −0.03 | −0.12 | −0.23 | −0.19 | −0.19 | −0.16 | −0.02 | 0.53[b] | 0.41[a] | 0.43[a] | −0.24 | −0.28 | −0.58[c] |
| DOC | −0.12 | 0.17 | −0.04 | 0.10 | −0.21 | −0.14 | −0.03 | −0.08 | 0.09 | 0.34 | 0.63[c] | 0.65[c] | 0.57[b] | 0.04 | −0.18 | −0.48[b] |
| DIC | −0.30 | 0.00 | −0.20 | −0.05 | −0.17 | −0.22 | −0.24 | −0.18 | −0.16 | −0.03 | 0.56[b] | 0.46[a] | 0.46[a] | −0.26 | −0.33 | −0.64[c] |
| $SO_4$ | −0.26 | 0.31 | −0.24 | 0.20 | −0.09 | −0.37[a] | −0.06 | −0.36 | 0.39[a] | 0.22 | 0.33 | 0.30 | 0.51[b] | 0.24 | 0.33 | 0.10 |
| F | −0.25 | 0.06 | −0.21 | 0.01 | −0.14 | −0.22 | −0.13 | −0.09 | −0.08 | 0.33 | 0.62[b] | 0.55[b] | 0.44[a] | −0.29 | −0.23 | −0.53[b] |
| $NH_4$ | −0.02 | 0.05 | 0.06 | −0.18 | 0.12 | 0.13 | −0.18 | 0.05 | 0.04 | −0.33 | −0.38[a] | −0.32 | −0.35 | −0.18 | 0.05 | 0.23 |
| Na | −0.08 | −0.04 | −0.05 | 0.18 | −0.07 | −0.16 | 0.08 | 0.05 | −0.24 | 0.17 | 0.41[a] | 0.48[b] | 0.14 | −0.02 | −0.07 | −0.17 |
| Ca | −0.31 | 0.02 | −0.23 | −0.03 | −0.12 | −0.24 | −0.20 | −0.19 | −0.16 | −0.03 | 0.54[b] | 0.42[a] | 0.44[a] | −0.24 | −0.28 | −0.58[c] |
| Mg | −0.36[a] | −0.02 | −0.20 | −0.18 | −0.14 | −0.24 | −0.40[a] | −0.21 | −0.09 | −0.06 | 0.51[b] | 0.43[a] | 0.39 | −0.44[a] | −0.37 | −0.63[c] |
| Al(ORG) | 0.37 | −0.01 | 0.15 | 0.14 | −0.12 | 0.24 | 0.47[a] | 0.24 | 0.06 | 0.10 | −0.23 | −0.23 | −0.10 | 0.36 | 0.12 | 0.16 |
| Fe | 0.01 | −0.05 | 0.09 | −0.08 | −0.39[a] | −0.05 | −0.24 | −0.03 | 0.13 | −0.03 | 0.22 | 0.39[a] | 0.27 | −0.26 | −0.42[a] | −0.48[b] |
| Zn | 0.38[a] | −0.13 | 0.23 | 0.01 | 0.06 | 0.31 | 0.25 | 0.38 | 0.00 | 0.07 | −0.57[b] | −0.49[b] | −0.46[b] | 0.13 | 0.22 | 0.48[b] |
| Mn | 0.32 | −0.16 | 0.16 | 0.04 | 0.04 | 0.25 | 0.22 | 0.28 | −0.01 | −0.17 | −0.73[c] | −0.60[c] | −0.59[c] | 0.02 | 0.19 | 0.52[b] |
| TEMP | 0.06 | 0.04 | 0.01 | −0.03 | 0.48[b] | −0.04 | 0.23 | −0.29 | 0.05 | 0.04 | 0.06 | −0.06 | −0.02 | 0.14 | 0.17 | 0.31 |
| TURB | −0.26 | 0.27 | −0.21 | 0.04 | −0.23 | −0.27 | −0.22 | −0.33 | 0.06 | 0.15 | 0.63[c] | 0.37[a] | 0.73[c] | 0.05 | −0.14 | −0.40[a] |
| Light | −0.69[c] | −0.02 | −0.63[b] | 0.36 | 0.18 | −0.55[b] | −0.08 | −0.63[b] | −0.07 | 0.32 | 0.16 | 0.16 | 0.02 | 0.01 | 0.50[a] | 0.47[a] |

[a] $p < 0.05$.
[b] $p < 0.01$
[c] $p < 0.001$

depth. Their depth distributions were nonlinear, and correlated to light penetration. Although light penetration was reduced for a period of time following liming, those taxa which remained after liming were found at the same depths at which they occurred prior to liming.

Most of the decrease in the total algal biovolume during the season after liming can be attributed to the decrease in *H. pumilus* at 7 m in 1985. This also contributed to the significant decrease in total cyanobacterial biovolume after liming, in conjunction with the reduction in *Anacystis* standing crop. The mat of *H. pumilus* was not eliminated postliming, but the total biomass was substantially lower. The biovolume at this depth was not replaced by any other species, resulting in an overall reduction of biovolume at this depth between the 2 yr. This suggests that conditions became unfavorable for this species, and not that it was out-competed under the new habitat conditions. In addition to an altered chemical environment, seasonal light penetration patterns with depth were much different during 1985 than prior seasons before calcite addition (Bukaveckas 1989). We are unable to conclude which factor or combination of factors, reduced light, liming or seasonal differences, caused the reduction of *H. pumilus* and prevented the establishment of a new population to replace it.

*Hapalosiphon pumilus* is known to occur in acidic habitats, particularly from mineral-poor dystrophic bogs (Prescott 1962; Flensburg and Sparling 1973). In the present study, the chemical parameters mostly highly correlated with its distribution were low base cation concentrations (calcium and magnesium) and high iron concentrations. One interpretation of these data would be that, if the hypothesis of Davis et al. (1986) is correct, and Woods Lake was an acidic, brownwater lake until the onset of anthropogenic acidic deposition, *H. pumilus* might have been a part of the natural flora of Woods Lake for a long time. This species may represent one which can persist in habitats which may have been acidic brownwater lakes and have been converted to clear water, acidic habitats by addition of strong acids due to atmospheric deposition.

In contrast, Oscillatoriaceae did not achieve the abundance seen in the *H. pumilus* community prior to liming. Such an occurrence has been characteristic of acidic, oligotrophic lakes. The early reports of the occurrence of Oscillatoriaceae in acidic lakes led to the hypothesis that these communities were favored by acidification. More recent data are less conclusive about the factors controlling the distribution of these communities. Growth of filamentous cyanobacteria was not enhanced by artificial acidification in studies by Turner et al. (1987), who also observed dominance of these forms in neutral reference lakes as well as in acidified lakes. Stevenson et al. (1985) did not find a strong correlation between the presence of Oscillatoriaceae and pH or ANC. Qualitative observations of Hultberg and Andersson (1982) indicated that these mats were negatively affected by liming; however, the Oscillatoriaceae in Woods Lake were not significantly affected by liming. These communities seem to occur in a variety of habitats where pH and alkalinity alone do not appear to control their distribution. The proliferation of these cyanobacteria seems not to be linked to pH, per se, but to a combination of physicochemical and possibly biological conditions associated with some, but not all, acidic lakes.

The total biovolume of the diatom community of the shallow sediments was not altered by the calcite addition. The lack of change in net accumulation of diatom biomass indicated that

either the growth rate of diatoms was unchanged by the liming or that a change in growth rate was balanced by a corresponding loss of biomass. Regardless of the factors involved, liming did not negatively influence the accumulation of biomass. Diatoms remained the dominant benthic algae in this habitat, however, the species composition of this flora was significantly altered. Distributions of diatom taxa are known to be strongly correlated with lake water pH. The pH preference, as well as preference for other water chemistry conditions, have been reported for many species of diatoms (Hustedt 1939; Merlainen 1967; Patrick 1977; Charles 1985; Davis and Anderson 1985). These are also the categories used in paleolimnological investigations using diatom remains to reconstruct the pH history of lakes (Charles 1985). All of the dominant living epipelic diatoms in Woods Lake, prior to liming, were either acidobiontic or acidophilic species (Charles 1985; Anderson et al. 1986). These included: *N. tenuicephala, N. subtilissima, F. acidobiontica, E. curvata*, and the dominant *Pinnularia* sp. (*P. abaujensis* var?). Frustules of all of these were also abundant in the surface sediment fractions of the cores analyzed by Davis et al. (1986). Other species which were common in the surface sediments were noted in the living diatom communities prior to liming, including: *Tabellaria quadriseptata* Knud., *T. flocculosa* (Roth) Kutz. var. *flocculosa, T. flocculosa* var. *linearis* Koppen, *Actinella punctata* Lewis, *Anomoeoneis serians* var. *brachysira* (Breb. *ex* Kutz.) Hust., *Eunotia incisa* W. Sm. *ex* Greg., *Frustulia rhomboides* var *saxonica* (Rabh.) DeT., *Stenopterobia intermedia* (Lewis) V. H. and *Surirella delicatissima* Lewis. Two of these, *A. serians* and *F. rhomboides*, seem to be over represented in the sedimentary assemblage as compared with the recorded living epipelic communities in 1984. This could be due to a reduction in these species in the living community subsequent to the collection of core samples in 1980 (Davis et al. 1986). However, the patchy epipelic growth of diatoms or occurrence as primarily epiphytic species can also cause over representation of taxa in deep-water sediments relative to living epipelon in shallow water (DeNicola 1986).

*Eunotia* spp. and *N. subtilissima* have both been abundant throughout the known 200-yr history of Woods Lake. The long-term distributions of these two species also agree with the data from the liming study. The relative abundance of both were not as reduced after liming as *F. acidobiontica* or *N. tenuicephala*. The total biovolume of *N. subtilissima* was lower in 1985 than the year before liming, but its distribution was not as strongly correlated to pH and ANC. The dominant species of *Eunotia, E. curvata*, was in both the present study and in the sedimentary fossil data of Davis et al. (1986). This species was not significantly reduced after liming and has also persisted throughout the lake's history, even in times thought to have elevated pH and ANC (Davis et al. 1986).

Two of the species which became dominant in the living benthic algal community after calcite addition were both present in the sedimentary record. *Anomoeoneis vitrea* and *Achnanthes microcephala* are both pH-indifferent species and reached peak abundance in Woods Lake 3 mo after liming. *Anomoeoneis vitrea* was present at very low percentages throughout the sediment core samples with an abrupt abundance peak in the region of the inferred pH increase due to watershed disturbance around 1860 (Charles 1985). *Achnanthes microcephala* was less than 1% of the preserved diatom community throughout the sedimentary record (Davis et al. 1986). This species commonly achieves numerical dominance in the littoral zones of oligotrophic lakes and prefers calcium-rich environments (Godward 1937; Patrick and Reimer 1966; Fox et al. 1969; Stockner and Armstrong 1971).

*Cymbella microcephala* was the only alkalophilic species which became abundant in the first season after liming. This species reached its highest relative abundance 7 wk after liming on shallow sediments when the pH and ANC just above the sediments were at their maximum values. As the pH and ANC declined over the summer, *C. microcephala* was replaced by the pH-indifferent forms.

Due to the time scale of the community response after liming, this study provides no evidence for grazing or alterations in decomposition processes as important factors in determining benthic algal biomass or community structure. The nature of the response of the epipelic algae to liming indicates that pH preference, especially among diatoms, was important in determining the community structure of the epipelon.

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# Effects of Neutralization and Addition of Brook Trout (*Salvelinus fontinalis*) on the Limnetic Zooplankton Communities of Two Acidic Lakes[1]

William R. Schaffner[2]

*Cooperative Fish and Wildlife Research Unit, Department of Natural Resources, Cornell University, Ithaca, NY 14833, USA*

Schaffner, W. R. 1989. Effects of neutralization and the addition of brook trout (*Salvelinus fontinalis*) on the limnetic zooplankton communities of two acidic lakes. Can. J. Fish. Aquat. Sci. 46: 295–305.

The zooplankton communities in two acidified lakes in the Adirondack region of New York changed considerably following liming and the reintroduction of brook trout (*Salvelinus fontinalis*). Most rotifer taxa were greatly reduced in numbers within a week following base addition. *Keratella taurocephala* declined by orders of magnitude in both lakes. Rotifer species that replaced *K. taurocephala* were far less abundant. The crustacean communities were also affected by liming. *Diaptomus minutus*, the dominant in both lakes, declined following base addition. Longer-term population responses appeared to be related to the dynamics of the individual populations, and changes in predation pressure. Four additional crustacean species became prominent in the lakes after liming: the caldocerans *Bosmina longirostris* and *Daphnia catawba* in Cranberry Pond, and *D. catawba* and the cyclopoid copepod *Cyclops scutifer* in Woods Lake. Over the longer-term liming and the introduction of brook trout tended to have an overall positive effect on the zooplankton communities in the two lakes.

On a constaté que les communautés zooplanktoniques ont considérablement changé dans deux lacs acidifiés des Adirondacks, dans l'État de New York, après un traitement au calcaire et la réintroduction d'ombles de fontaine (*Salvelinus fontinalis*). La plupart des taxons de rotifères ont été considérablement réduits durant la semaine qui a suivi l'application de la base. Le nombre de *Keratella taurocephala* a baissé de plusieurs ordres de grandeur dans les deux lacs. Les espèces de rotifères qui l'ont remplacé étaient beaucoup moins abondantes. Les crustacés ont aussi été touchés par le traitement. Le nombre de *Diaptomus minutus*, espèce dominante dans les deux lacs, a baissé après le traitement. Il semble que les réactions à plus long terme soient reliées à la dynamique de chacune des populations et aux changements des caractéristiques de la prédation. Après le traitement, quatre autres espèces de crustacés ont pris de l'importance dans les lacs : les cladocères *Bosmina longirostris* et *Daphnia catawba*, dans l'étang Cranberry, ainsi que *D. catawba* et le copépode cyclopoïde *Cyclops scutifer*, dans le lac Woods. À long terme, l'application de la base et l'introduction d'ombles de fontaine ont eu sur les communautés zooplanktoniques des deux lacs des effets généralement bénéfiques.

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Zooplankton communities in recently acidified lakes are usually characterized by relatively few species (Confer et al. 1983) with rotifers, copepods, and small cladocerans being the most prevalent forms (Eriksson et al. 1982; Hasselrot et al. 1984; Hasselrot and Hultberg 1984; Keller and Pitblado 1984). The conditions that produce such communities often have direct physiological links with pH (Havas and Hutchinson 1982; Malley et al. 1982; Havas and Likens 1985), but more complicated processes such as changes in competition and predation can also play a role (Kajak and Ranke-Rybicka 1970; Fedorenko 1975; Gliwicz et al. 1978; Kajak and Rybak 1979; Lynch 1979; Neill 1981). Lake liming to mitigate acidification, and the reintroduction of fish have the potential to reverse these changes but results to date have been inconclusive with various investigators reporting a variety of responses to lake liming (Hultberg and Andersson 1981; Eriksson et al. 1983; Hasselrot et al. 1984; Hasselrot and Hultberg 1984).

Our objectives were (1) to define the structure and dynamics of the zooplankton communities in two acidified, fishless lakes in the Adirondack region of New York, (2) document the changes, both immediate and longer term, that occurred after liming and the reintroduction of fish (Porcella 1989), and (3) to attempt to identify wherever possible the causal mechanisms that underlay the observed changes.

## Materials and Methods

### Sampling

The study sites were two acidified, fishless lakes in the Adirondack region of New York, Cranberry Pond, the smaller

[1]This is part of a series of 13 papers devoted to the Lake Acidification Mitigation Project.

[2]Present address: Section of Ecology and Systematics, Cornell University, Ithaca, NY 14853, USA.

of the two, had a surface area of 7.2 ha, a volume of 2.07 × $10^5$ $m^3$, and a mean water residence time of 63 d. Maximum and mean depths are 7.9 and 2.9 m, respectively. Woods Lake had a surface area of 23 ha, a volume of 8.0 × $10^5$ $m^3$, a mean water residence time of 174 d, and maximum and mean depths of 12.0 and 3.5 m. A detailed description of the lake basins and their hydrology can be found in Staubitz and Zarriello (1989).

Samples were collected at four stations in Woods Lake along a longitudinal axis that passed through the deepest portion. Stations depths were 4.5, 7.0, 12.0, and 6.0 m on a heading from the inlet to the outlet. Cranberry Pond was sampled at three stations with depths of 3.0, 5.0, and 7.0 m located in a triangular pattern. Duplicate vertical tows were made at each station at approximately 3-wk intervals for a period of 3 yr. Additional samples were obtained just before and 1 wk after base addition. Collections were made during daylight hours with an unmetered 30-cm diameter net with an 80-μm mesh size and a 5:1 length–diameter ratio. Tows were started from 1 m above the bottom, and sample volume was estimated from the area of the net mouth and the length of the tow. Temperature measurements were made at the same time at 0.5-m intervals from surface to bottom at the deepest station.

In an effort to estimate overall efficiency of the net tows and the retention of rotifers, tows were compared with samples collected with a 30-L Schindler–Patalas trap equipped with a 60-μm mesh net on dates when zooplankton were reasonably abundant. In general, the trap was more efficient than the net (Table 1). The data from Cranberry Pond are thought to be more reliable estimates, as the trap sampling depths were closer together.

Preserved samples (ca. 4% formalin solution) were concentrated to known volumes to facilitate counting. One millilitre subsamples were removed from the samples with a large bore pipette and transferred to a Sedgewick–Rafter cell. The whole chamber was enumerated using a compound microscope at a magnification of 40 or 100×. In most instances 100 or more organisms were counted per subsample (Edmondson and Winberg 1971). When necessary, species identification (except for certain rotifers, e.g. *Polyarthra* and *Synchaeta*, and some immature crustaceans) was verified at a higher magnification. Identifications were based on standard taxonomic references: Herrick and Turner 1885; Brooks 1959; Edmondson 1963; Ruttner-Kolisko 1974; Koste 1978. Copepod developmental stages were divided into six groups; males, females, *CV* and *CIV* (late copepodids), *CIII-CI* (early copepodids), *NVI/NV-NIV* (late nauplii), and *NIII-NI* (early nauplii). Schindler–Patalas trap samples were composited for each depth profile, and enumerated as above. Numbers reported in the text are the mean ± SE.

Population estimates and egg numbers are the means of all counts made for a given date. No adjustments were made for net sampling efficiency. Mean egg clutch size was estimated from all the clusters seen over the time interval being considered. Eggs·female$^{-1}$ ratios were based on all the eggs and females counted on a given sampling date.

## Results

### Cranberry Pond

Of the two lakes, Cranberry Pond had the fewer zooplankton species. As in numerous other acidified lakes (Yan and Geiling 1985; Siegfried et al. 1984; Roff and Kwiatkowski 1977) *Keratella taurocephala* was the dominant rotifer prior to liming. In 1984 the species was abundant from mid-May through October, but much reduced at other times (Fig. 1). Peaks occurred in early June (455 ± 54.7 × $10^3$ individuals·$m^{-3}$) and mid-September (182 ± 19.6 × $10^3$ individuals·$m^{-3}$). Growth was similar in 1985. A population of 206 ± 24.1 × $10^3$ individuals·$m^{-3}$ was present by May 28 just before liming. Numbers declined rapidly after base addition. *K. taurocephala* was again the dominant rotifer in 1986, but the population was smaller than the previous 2 yr with a maximum of 98.4 ± 25.3 × $10^3$ individuals·$m^{-3}$ in mid-July.

Seven additional rotifer taxa were encountered with reasonable frequency prior to liming (Table 2). *Synchaeta* was the most abundant, dominating when *K. taurocephala* standing stocks were low. All taxa declined markedly after base addition, but *Polyarthra* eventually increased and dominated the rotifer community during the latter part of 1985.

TABLE 1. Means of all tow and composite trap samples collected in Cranberry Pond and Woods Lake to compare the sampling efficiency of vertical net hauls versus the Schindler – Patalas trap. Schindler – Patalas trap samples were collected at 1-m intervals in Cranberry Pond, and from the epi-, meta-, and hypolimnion in Woods Lake. Means are in individuals·$m^{-3}$. Cope = copepodids, Naup = nauplii, Bl = *Bosmina longirostris*, Kt = *Keratella taurocephala*, Syn = *Synchaeta*, Ploe = *Ploesoma*, Poly = *Polyarthra*, Rot = all other rotifers.

| | | Net | | | Trap | | | Net:Trap |
|---|---|---|---|---|---|---|---|---|
| | | $\bar{X}$ | $s$ | $N$ | $\bar{X}$ | $s$ | $N$ | ×100 |
| Cranberry Pond | Cope | 43,562 | 15,842 | 24 | 64,554 | 20,249 | 24 | 67.5 |
| | Naup | 15,040 | 15,965 | 24 | 23,072 | 24,254 | 24 | 65.2 |
| | Bl | 8,020 | 4,186 | 12 | 8,462 | 2,817 | 12 | 94.8 |
| | Kt | 49,996 | 54,903 | 24 | 77,968 | 82,806 | 24 | 64.1 |
| | Syn | 18,100 | 3,332 | 8 | 5,774 | 3,541 | 8 | 313 |
| | Ploe | 4,238 | 3,653 | 8 | 6,628 | 5,062 | 8 | 63.9 |
| | Rot | 2,487 | 1,508 | 12 | 2,404 | 1,223 | 12 | 103 |
| Woods Lake | Cope | 35,207 | 9,766 | 12 | 39,546 | 12,350 | 12 | 89.0 |
| | Naup | 11,123 | 6,986 | 12 | 17,759 | 14,413 | 12 | 62.6 |
| | Bl | 9,758 | 4,366 | 12 | 2,184 | 2,379 | 12 | 410 |
| | Kt | 77,046 | 29,817 | 12 | 123,349 | 31,043 | 12 | 62.5 |
| | Poly | 9,531 | 8,353 | 12 | 2,976 | 2,251 | 12 | 320 |
| | Rot | 2,971 | 4,505 | 12 | 4,039 | 4,546 | 12 | 73.6 |

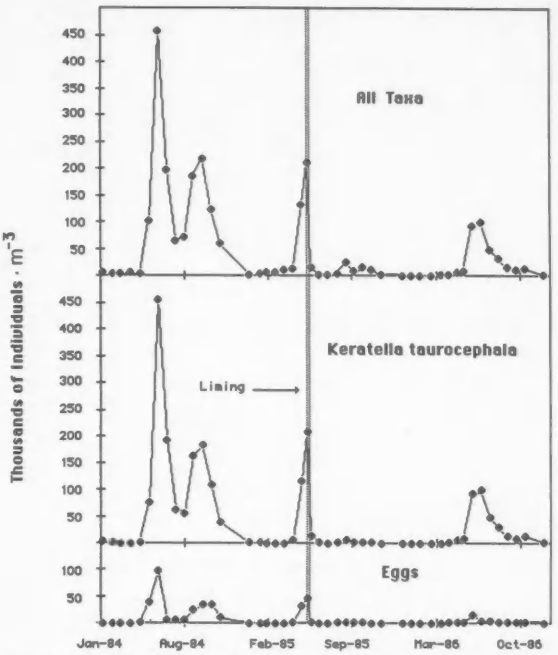


FIG. 1. Mean densities of all rotifer taxa and *Keratella taurocephala* during 1984–86 in Cranberry Pond.

The preliming crustacean zooplankton community was essentially composed of two calanoid copepods, *Diaptomus minutus* and *D. leptopus*. Of the two, *D. minutus* was by far the more numerous. This species is widely distributed and common to many New York lakes (Hall and Waterman 1968, 1967), and appears to be highly successful in adapting to acidic conditions (Sprules 1975; Bleiwas et al. 1984; Keller and Pitblado 1984). Population growth of *D. minutus* in Cranberry Pond was unusual in that it was characterized by the appearance of nauplii in late April that apparently hatched from diapause eggs, as the adults that were present and the eggs that they produced did not seem to be abundant enough to account for the large population of young (Fig. 2).

Base addition to Cranberry Pond had a significant effect on the *D. minutus* population. Numbers had increased to 48.7 $\pm$ 6.2 $\times$ $10^3$ individuals·$m^{-3}$ by May 28, 1985 with 21.0 $\pm$ 1.8 $\times$ $10^3$ eggs·$m^{-3}$, but by June 6 the population had declined to 32.5 $\pm$ 0.8 $\times$ $10^3$ individuals·$m^{-3}$, and eggs were below detection. Standing stock continued to decline, and were reduced to 18.0 $\pm$ 3.0 $\times$ $10^3$ individuals·$m^{-3}$ by late June; only 30% of the 59.7 $\pm$ 2.6 $\times$ $10^3$ individuals·$m^{-3}$ present in late June 1984. The most noticeable losses were to the new generation that was just beginning to develop (i.e. eggs and immature stages); adults appeared to be little affected. Numbers increased somewhat by mid-July following the resumption of egg production in late June, but dropped after that even though egg production continued through September.

*Diaptomus minutus* returned to prominance in 1986 following the appearance of nauplii in late April. Eggs were below detection at this time. The mid-July population maximum of 83.6 $\pm$ 2.4 individuals·$m^{-3}$ was considerably lower than the 1984 mid-July peak of 147 $\pm$ 8.6 $\times$ $10^3$ individuals·$m^{-3}$. Mean egg clutch size and the ratio of eggs·female$^{-1}$ were also considerably lower when 1986 is compared with 1984 (Table 3). The most striking change in the 1986 *D. minutus* population was the large number of adults that persisted into the winter months.

The other diaptomid found in Cranberry Pond, *D. leptopus* (Fig. 3), has been widely reported from coast to coast in the northern United States and Canada, and occurs in habitats ranging from acid bogs to alkaline ponds (Winner 1970). Base addition did not appear to affect *D. leptopus*. Egg production which was initiated in April continued through August. Numbers peaked at 13.2 $\pm$ 2.0 $\times$ $10^3$ individuals·$m^{-3}$ in mid-September. The population began to increase again (with the appearance of adults and copepodids) in early January 1986, and had reached a level of 22.1 $\pm$ 1.2 $\times$ $10^3$ individuals·$m^{-3}$ by mid-February. But standing stocks were markedly reduced by mid-March. Eggs and nauplii that were observed in April seemed to have little effect on the population, and by late October only a few individuals remained in the water column.

Two cladocerans appeared in significant amounts after liming. *Daphnia catawba*, which had not been observed in the lake prior to base addition, was first noted in late August as an immature *Daphnia*. The species was most abundant in September and October, but few eggs were noted (Fig. 4). The mid-September population was mostly immature stages, and that of early October was comprised of 80% males. The species reappeared in 1986, but was less numerous than in 1985.

The second cladoceran, *Bosmina longirostris*, had been observed on three sampling dates prior to liming, but at numbers just above the limits of detection. The species appeared with *D. catawba* in late August 1985 (Fig. 4), but was considerably less abundant. *Bosmina* was present throughout most of 1986, and was most numerous in June and July with a maximum of 39.1 $\pm$ 9.5 $\times$ $10^3$ individuals·$m^{-3}$ in mid-June.

Mean epilimnetic temperatures tended to be cooler in 1985 and 1986 than in 1984 (Table 4).

## Woods Lake

The most abundant of the eight rotifer taxa that were observed in Woods Lake prior to liming was *K. taurocephala*. The species was most numerous during the warmer months with a minimum in March and April (Fig. 5). An early June 1984 peak (108 $\pm$ 18.5 $\times$ $10^3$ individuals·$m^{-3}$) was followed by a larger one in August (158 $\pm$ 10.2 $\times$ $10^3$ individuals·$m^{-3}$). Population growth in 1985 appeared to be similar to 1984 in that mid-May standing stocks were comparable. By late May 1985 the population had increased to 56.3 $\pm$ 8.3 $\times$ $10^3$ individuals·$m^{-3}$. Numbers decreased dramatically following base addition. Standing stocks remained low in 1986 when *K. taurocephala* was only a minor component of the zooplankton community.

A second *Keratella* species, *K. hiemalis*, was most abundant in the spring during the *K. taurocephala* minimum (Table 5). *Keratella hiemalis* did not appear to be affected by liming, but the population was declining at the time of base addition. The species was considerably more numerous in January 1986 than it had been the previous 2 yr, and eventually reached a late April maximum of 17.2 $\pm$ 3.9 $\times$ $10^3$ individuals·$m^{-3}$ that was four times greater than the 1984 and 1985 peaks.

*Polyarthra* was second in abundance prior to liming (Table 5), and peaked concurrently with *K. taurocephala* in August 1984 at 27.8 $\pm$ 2.9 $\times$ $10^3$ individuals·$m^{-3}$. *Polyarthra* was increasing before liming in 1985, but declined sharply thereafter. The species reappeared in early August 1985, and

TABLE 2. Cranberry Pond rotifers mean number of individuals·m$^{-3}$ in thousands.

1984

| | 1–28 | 2–18 | 3–9 | 3–31 | 4–24 | 5–16 | 6–6 | 6–27 | 7–18 | 8–8 | 8–29 | 9–19 | 10–10 | 10–31 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Synchaeta* | 2.09 | 2.05 | 2.69 | 5.70 | 0.03 | 25.3 | 0.98 | 0.36 | 0.75 | 3.36 | 10.3 | 28.0 | 10.1 | 15.7 |
| *Polyarthra* | 0.02 | | | | | 0.60 | 0.34 | 0.33 | 0.19 | 0.10 | 1.58 | 3.88 | 1.56 | 4.88 |
| *Trichocerca multicrinis* | | | | | | 0.12 | 0.85 | 3.33 | 1.78 | 0.41 | 0.31 | 2.05 | 0.36 | 0.05 |
| *Monostyla lunaris* | | 0.03 | 0.09 | | 0.05 | 0.05 | | | | 0.03 | 0.05 | 0.11 | 0.22 | 0.22 |
| *Collotheca* | | | | | | | | | | 3.16 | 1.47 | 0.58 | 0.90 | 0.02 |
| *Ploesoma* | | | | | | | | | | 4.43 | 10.2 | 2.68 | 0.06 | |
| *Lecana* | | | | | 0.01 | 0.08 | | | | 0.20 | 0.08 | 0.08 | 0.10 | |

1985

| | 1–9 | 2–4 | 2–20 | 3–12 | 4–2 | 4–23 | 5–14 | 5–28 | 6–6 | 6–25 | 7–16 | 8–6 | 8–27 | 9–16 | 10–7 | 10–28 | 11–19 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Synchaeta* | 3.93 | 3.72 | 4.58 | 6.40 | 9.62 | 6.12 | 16.2 | 2.14 | 0.23 | 0.08 | 0.02 | | | | 0.02 | 0.01 | 0.19 |
| *Polyarthra* | 0.03 | 0.01 | 0.02 | | 0.01 | 0.01 | 0.85 | 1.46 | | | 0.02 | 2.26 | 19.1 | 6.42 | 13.4 | 10.5 | 1.42 |
| *Trichocerca multicrinis* | | | | | | | 0.42 | 0.20 | | | 0.02 | | | | | | |
| *Monostyla lunaris* | | | 0.01 | 0.04 | | 0.05 | 0.01 | | 0.37 | 0.03 | 0.02 | 0.02 | 0.06 | 0.03 | 0.02 | 0.03 | |
| *Collotheca* | | | | | | | | | | | | | | | | | |
| *Ploesoma* | | | | | | | | | | | | | | | | | |
| *Lecana* | 0.06 | | 0.01 | 0.04 | | 0.06 | 0.08 | | 0.10 | 0.01 | | | 0.01 | | 0.04 | | |

1986

| | 1–8 | 1–30 | 2–20 | 3–18 | 4–10 | 4–28 | 5–19 | 6–3 | 6–24 | 7–14 | 8–4 | 8–25 | 9–15 | 10–6 | 10–28 | 12–12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Synchaeta* | | 0.04 | 0.06 | 0.11 | 0.05 | 0.22 | 0.01 | 0.02 | | | | 0.11 | 0.06 | 0.06 | 0.07 | 0.13 |
| *Polyarthra* | | 0.01 | | | | 0.03 | 0.01 | 0.02 | 0.11 | 1.81 | 0.28 | 0.63 | 0.59 | 0.51 | 0.07 | 0.01 |
| *Trichocerca multicrinis* | | | | | | 0.01 | | | | 0.07 | 0.13 | 1.11 | 0.56 | | | |
| *Monostyla lunaris* | | | | | | 0.02 | | 0.02 | 0.02 | 0.11 | | 0.03 | 0.07 | 0.09 | 0.06 | 0.05 |
| *Collotheca* | | | | | | | | | | | | 0.02 | 0.08 | 0.12 | 0.01 | |
| *Ploesoma* | | | | | | | | | | | 0.01 | | 0.02 | 0.06 | | |
| *Lecana* | | | | | | | 0.01 | | 0.03 | 0.04 | | 0.02 | 0.04 | 0.10 | 0.07 | 0.06 |

was the dominant rotifer in October. The species peaked in June in 1986, but declined after that. Rotifers in general were scarce during July and August, that year.

Of the four remaining taxa, *Trichocerca multicrinis* was present in 1984 and 1985, but did not reappear after liming. *Collotheca* was the third most abundant taxon in 1984, and was the dominant form in early September 1986. *Synchaeta* was sporadic in 1984, but was encountered more frequently in 1985 and 1986. In general, all of the taxa declined during the immediate postliming period (Table 5).

Prior to liming the crustacean zooplankton community in Woods Lake was characterized by three species: *D. minutus*, *B. longirostris*, and the cyclopoid copepod *Mesocyclops edax*.

As in Cranberry Pond, *D. minutus* was the dominant crustacean, but the species differed from its Cranberry Pond counterpart in that the spring cohort of nauplii hatched from eggs produced by over-wintering adults. There was no evidence for the hatching of diapause eggs. In 1984, eggs were observed by mid-March, nauplii appeared in early June, and adults in late June. These new adults produced the eggs that eventually gave rise to the next generation of over-wintering adults (Fig. 6). Egg production was initiated earlier in 1985, and was essentially completed before liming. Standing stocks in mid-May 1985 were very similar to 1984 but were more advanced developmentally in 1985 due to the earlier egg production. Numbers had increased to 34.6 ± 3.0 × 10$^3$ individuals by late May 1985, and appeared to be leveling off as egg production had almost ceased. The population was reduced by 59% the week following base addition. Nauplii and early copepodids accounted for almost all of the losses. Egg production was resumed in late June, and continued through the winter and into the summer of 1986. This resulted in a gradual increase in numbers through the remainder of 1985 and the first half of 1986. But by early June a decline set in which culminated in the population being reduced to barely detectable levels by July and August. Losses were primarily in the early stages (nauplii and early copepodids), as the later stages continued to increase in number. The few adults that were present continued to produce eggs at a rate considerably greater than during the preliming period (Table 6).

The predatory cyclopoid copepod *M. edax* was most numerous during the summer, apparently diapausing on the bottom as an immature copepodid during the colder months (Fig. 7). In 1984 eggs were produced from May through August. The population peaked in August at 27.5 ± 0.9 × 10$^3$ individuals·m$^{-3}$. The 1985 population seemed to be off to a similar start, but declined following base addition primarily due to a decrease in nauplii and the cessation of egg production. Growth was resumed in August in conjunction with increased egg abundance. The species reappeared in 1986, and peaked much earlier than in either 1984 or 1985 with a maximum in mid-June of 26.7 ± 1.6 × 10$^3$ individuals·m$^{-3}$.

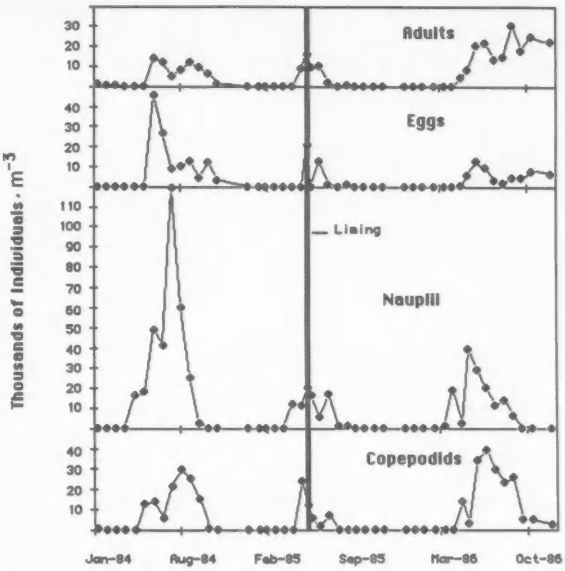


FIG. 2. Mean *Diaptomus minutus* densities during 1984–86 in Cranberry Pond.

TABLE 3. Cranberry Pond *Diaptomus minutus* mean egg clutch size and eggs·female$^{-1}$ ratio 1984–86.

| Egg clutch size | Mean | SE |
|---|---|---|
| 1984 Annual | 6.1 | 0.08 |
| Maximum (6 June) | 11.0 | 0.2 |
| Minimum (19 Sept.) | 3.4 | 0.1 |
| 1985 Annual | 4.8 | 0.1 |
| Maximum (6 Aug.) | 16.0 | (one cluster) |
| Minimum (16 July) | 3.7 | 0.2 |
| 1986 Annual | 2.2 | 0.03 |
| Maximum (16 May) | 7.1 | 0.3 |
| Minimum (15 Sept.) | 1.6 | 0.04 |
| Eggs·female$^{-1}$ | | |
| 1984 Annual | 3.2 | 0.8 |
| Maximum (6 June) | 7.9 | |
| Miminum (19 Sept.) | 1.1 | |
| 1985 Preliming | 8.2 | 3.8 |
| Maximum (14 May) | 12.0 | |
| Minimum (28 May) | 4.5 | |
| Postliming | 2.2 | 0.6 |
| Maximum (27 Aug.) | 3.7 | |
| Minimum (6 June) | 0.04 | |
| 1986 Annual | 0.8 | 0.2 |
| Maximum (3 June) | 2.0 | |
| Minimum (15 Sept.) | 0.3 | |

The cladoceran *B. longirostris* was present year-round in Woods Lake (Fig. 8). In 1984 the population reached a maximum of 21.7 ± 1.4 × $10^3$ individuals·$m^{-3}$ during a July–August peak. Eggs were present from mid-May through October, and were most abundant in mid-July. The 1985 population appeared to be off to a better start, but numbers dropped sharply following base addition, with a decline of about 90% during the first week. Egg production appeared to cease after liming, and was not resumed to any degree until August. The species had a bimodal distribution in 1986.

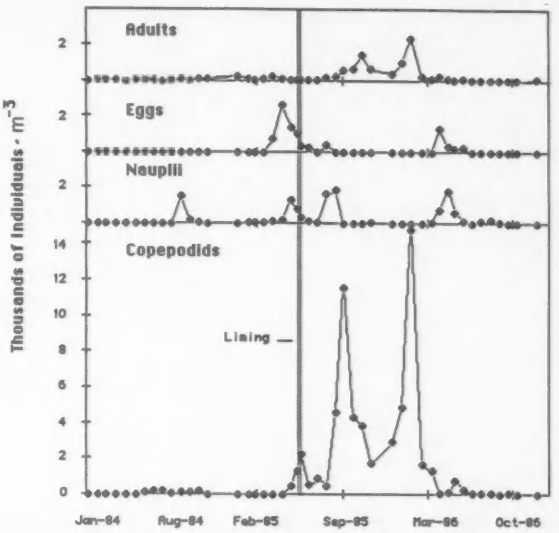


FIG. 3. Mean *Diaptomus leptopus* densities during 1984–86 in Cranberry Pond.

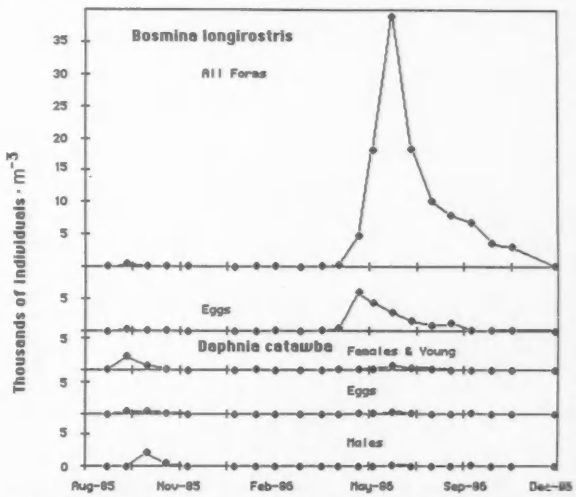


FIG. 4. Mean densities of *Bosmina longirostris* and *Daphnia catawba* during 1984–86 in Cranberry Pond.

Two additional crustaceans appeared in Woods Lake after liming. They were the cladoceran *Daphnia catawba*, and the cyclopoid copepod *Cyclops scutifer*. *Daphnia catawba* had not been observed in the lake prior to its appearance in mid-September 1985. A modest population was present until April 1986 when the species dropped below detection (Fig. 8). Egg-bearing females reappeared in mid-July 1986, and numbers peaked in early August at 15.5 ± 2.3 × $10^3$ individuals·$m^{-3}$. Males were present by mid-September. Ephippia were noted through November.

*Cyclops scutifer*, which has been observed in various Adirondack lakes (Hall and Waterman 1968) is common to cold, slightly acidic to near neutral waters (Keller and Pitblado 1984). The species was noted in Woods Lake on only three occasions prior to liming. A few individuals, mostly early copepodids,

TABLE 4. Mean temperature of epilimnion (centigrade) in Cranberry Pond (Station CO5) and Woods Lake (Station WO7) 1984–86.

| | Cranberry Pond | | | Woods Lake | | |
|---|---|---|---|---|---|---|
| Date | Mean | SE | Depth (m) | Mean | SE | Depth (m) |
| 1984 4 Jun | 16.5 | 0.92 | 3.5 | 13.6 | 0.22 | 7.5 |
| 25 Jun | 19.2 | 0.14 | 4.0 | 20.0 | 0.19 | 7.0 |
| 16 Jul | 22.3 | 0.11 | 4.5 | 22.7 | 0.18 | 8.0 |
| 6 Aug | 23.4 | 0.37 | 6.5 | 23.2 | 0.17 | 8.5 |
| 27 Aug | 21.1 | 0.17 | 6.5 | 21.1 | 0.09 | 10.5 |
| 1985 5 Jun | 15.8 | 0.70 | 4.5 | 17.1 | 0.30 | 6.0 |
| 24 Jun | 17.4 | 0.64 | 4.5 | 18.1 | 0.42 | 6.5 |
| 15 Jul | 19.5 | 0.81 | 5.0 | 19.8 | 0.38 | 6.5 |
| 5 Aug | 21.9 | 0.46 | 4.5 | 21.5 | 0.20 | 6.5 |
| 26 Aug | 18.2 | 0.18 | 5.5 | 19.4 | 0.14 | 7.5 |
| 1986 4 Jun | | No data | | 17.5 | 0.09 | 4.5 |
| 24 Jun | 16.8 | 0.31 | 4.5 | 19.6 | 0.30 | 5.5 |
| 14 Jul | 18.5 | 0.12 | 5.5 | 19.4 | 0.16 | 6.0 |
| 4 Aug | 20.9 | 0.37 | 5.0 | 21.2 | 0.28 | 6.0 |
| 25 Aug | 18.1 | 0.21 | 6.5 | 18.2 | 0.14 | 7.0 |

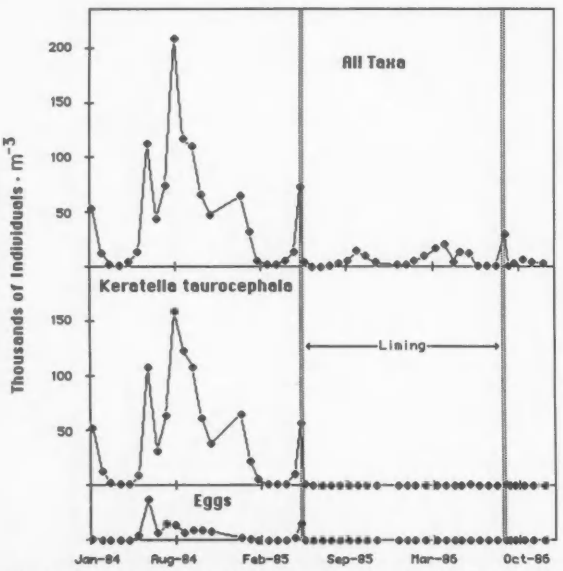


FIG. 5. Mean densities of all rotifer taxa and *Keratella taurocephala* during 1984–86 in Woods Lake.

appeared during June and July 1985 following neutralization, but the species dropped below detection after that. Early and late copepodids were again observed in January 1986, but egg production did not occur until mid-May. The population peaked in mid-July ($2.8 \pm 1.1 \times 10^3$ individuals·$m^{-3}$), with a majority of the animals being collected at the deepest station, suggesting that most individuals were inhabiting the cold deeper portion of the lake. Development appeared to be slow, as by late November the population was composed of 11% late copepodids, 67% early copepodids, and 19% nauplii.

As in Cranberry Pond mean epilimnetic temperatures in Woods Lake tended to be cooler in 1985 and 1986 than in 1984 (Table 4).

## Discussion

Prior to neutralization both Woods Lake and Cranberry Pond had zooplankton communities characteristic of acidified lakes (Eriksson et al. 1982; Hasselrot and Hultberg 1984; Hasselrot et al. 1984; Keller and Pitblado 1984). A somewhat greater species richness in Woods Lake was primarily attributed to the presence of *Chaoborus punctipennis* in Woods Lake (M. Robbins, Indiana University, pers. comm.) versus *C. americanus* in Cranberry Pond (Evans 1989). Both species prey on zooplankton, but migrating forms such as *C. punctipennis* tend to be less effective predators than those that are wholely pelagic in habit like *C. americanus* (Stenson et al. 1978). Since nonmigrating species are far more sensitive to fish predation (Northcote et al. 1978; Stenson et al. 1978) the presence of the two different taxa was probably more related to the historical presence of fish in the study lakes than conditions associated with low pH (Evans 1989).

Even though liming and the addition of fish did not for the most part appear to have permanent deleterious affects on the zooplankton communities; zooplankton abundances changed dramatically in both lakes. The interactions that produced the changes were often complex, and sometimes subtle in nature. Of primary importance were: a large rapid rise in lake pH from below 5.0 to, initially, about 9.0 (Fordham and Driscoll 1989); a decline in phytoplankton standing crop (Bukaveckas 1989); and modifications in predator–prey interactions.

Essentially all rotifer taxa declined following base addition, but the most striking changes involved *K. taurocephala* which was reduced by 93–97% within a week of liming. Similar responses have been noted by others and were probably due to a rapid rise in pH, as the species appears to be restricted to acidic bodies of water (Roff and Kwiatkowski 1977; Siegfried et al. 1984). A reduction in food availability may also have contributed to the declines in Cranberry Pond and Woods Lake as egg production also stopped. The fact that neither population made a comeback in 1985 while the pH remained above 7.0 (Fordham and Driscoll 1989), even though phytoplankton standing crops increased in July (Bukaveckas 1989), lends support to the argument that pH was the primary controlling factor. In addition, *K. taurocephala* reestablishing itself in Cranberry Pond in 1986 after the lake reacidified to preliming levels. The species continued to be rare in Woods Lake where the pH was still elevated.

Unlike *K. taurocephala, Polyarthra* was able to overcome its initial postliming decline relatively quickly, and increased in abundance during the latter part of 1985. By this time the water column pH had stabilized, and phytoplankton standing stocks had increased. Similar postliming responses have been observed by others and in some instances have been attributed to increased food availability (Henrikson et al. 1985). Additional factors such as greatly reduced competition with *K. taurocephala*, a decline in the predatory rotifer *Synchaeta* (Comita 1972; Hutchinson 1967), and a lessening of *Chaoborus* predation (Foran and King 1982; Moore and Gilbert 1987) due to brook trout (*Salvelinus fontinalis*) feeding on the larvae (Evans 1989; Gloss et al. 1989) may also have enhanced the success of *Polyarthra*. Nonetheless, it was not able to replace *K. taurocephala* in numerical abundance.

As in other studies (e.g. Scheider et al. 1975), crustaceans also declined during the immediate postliming period. Large, rapid increases in pH following neutralization have been implicated in zooplankton mortality (Scheider et al. 1975), whereas smaller, gradual changes seemed to be less harmful (Scheider and Dillon 1976). The species present in Cranberry Pond and Woods Lake (i.e. *B. longirostris, M. edax*, and *D. minutus*) are not limited by pH, and are widely distributed in New York state

TABLE 5. Woods Lake rotifers (mean number of individuals·m$^{-3}$ in thousands).

1984

| | 1–27 | 2–18 | 3–9 | 3–31 | 4–23 | 5–14 | 6–4 | 6–25 | 7–16 | 8–6 | 8–27 | 9–17 | 10–8 | 10–29 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Keratella hiemalis* | | | 0.03 | 0.06 | 3.70 | 3.76 | 1.74 | | | | | | | |
| *Synchaeta* | | | | | | | 0.11 | 2.32 | | | 0.09 | 0.03 | | 0.04 |
| *Polyarthra* | | | | | | 0.02 | 0.36 | 1.32 | 7.16 | 27.9 | 13.4 | 2.70 | 1.81 | 3.57 |
| *Trichocerca multicrinis* | | | | | | 0.25 | 0.79 | 9.36 | 0.18 | 4.57 | 0.79 | 0.25 | 0.41 | 0.21 |
| *Monostyla lunaris* | 0.05 | 0.02 | 0.02 | 0.04 | 0.01 | 0.03 | 0.04 | 0.01 | 0.22 | | 0.01 | | | 0.04 |
| *Collotheca* | | | | | | | 0.03 | | 2.57 | 14.4 | 0.29 | 0.14 | 0.06 | 0.01 |
| *Gastropus stylifer* | | | | | | | | | | | | | | |

1985

| | 1–7 | 1–29 | 2–17 | 3–11 | 4–1 | 4–22 | 5–13 | 5–28 | 6–5 | 6–24 | 7–15 | 8–5 | 8–26 | 9–16 | 10–7 | 10–28 | 11–18 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Keratella hiemalis* | 0.04 | 0.01 | 0.08 | 0.54 | 0.98 | 3.25 | 0.81 | 1.09 | 0.34 | 0.03 | 0.07 | 0.01 | 0.18 | | | | 0.13 |
| *Synchaeta* | 0.03 | 0.01 | | 0.22 | 0.26 | 0.56 | 2.36 | 13.6 | 3.42 | 0.06 | 0.02 | 0.02 | 0.03 | | 0.01 | 0.20 | 0.59 |
| *Polyarthra* | 0.09 | 0.02 | | | | 0.08 | 1.03 | 2.70 | 0.22 | | | 0.04 | 0.64 | 4.10 | 14.1 | 8.00 | 2.75 |
| *Trichocerca multicrinis* | | | | | | | 0.08 | 0.15 | 0.12 | | | | | | | | |
| *Monostyla lunaris* | 0.02 | 0.01 | 0.03 | 0.03 | | 0.01 | 0.02 | 0.02 | 0.07 | | | 0.17 | 1.63 | 0.80 | 0.32 | 0.09 | 0.004 |
| *Collotheca* | | | | | | | | | | | | | | 0.01 | 0.17 | 1.21 | 0.49 |
| *Gastropus stylifer* | | | | | | | | | | | | | | | | | |

1986

| | 1–10 | 1–30 | 2–17 | 3–13 | 4–8 | 4–28 | 5–19 | 6–4 | 6–24 | 7–14 | 8–4 | 8–25 | 9–15 | 9–24 | 10–6 | 10–28 | 11–17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Keratella hiemalis* | 1.37 | 1.55 | 5.05 | 7.35 | 13.5 | 16.9 | 0.50 | 0.72 | 0.25 | | | | | | | 0.003 | 0.37 |
| *Synchaeta* | 0.18 | 0.26 | 0.54 | 2.15 | 3.06 | 0.97 | 0.33 | 0.69 | 0.12 | 0.03 | | 0.01 | 0.03 | 0.01 | 0.02 | 0.13 | 0.12 |
| *Polyarthra* | | | | | | 0.07 | 1.08 | 5.42 | 10.6 | 0.03 | 0.04 | 0.02 | 3.08 | 0.83 | 2.62 | 6.35 | 3.96 |
| *Trichocerca multicrinis* | | | | | | | | | | | | | | | | | |
| *Monostyla lunaris* | | | | 0.01 | 0.01 | 0.05 | 0.05 | 0.08 | 0.02 | | | | 0.02 | 0.01 | 0.004 | 0.02 | 0.01 |
| *Collotheca* | | | | 0.11 | | 0.003 | 0.13 | 4.07 | 0.18 | | | 0.13 | 21.0 | | | | |
| *Gastropus stylifer* | | | | | | 0.01 | 2.02 | 3.25 | 1.15 | 0.01 | 0.01 | | 0.03 | | | | 0.01 |

(Hall and Waterman 1967, 1986) and elsewhere. But some developmental stages may be more sensitive than others to conditions associated with base addition. The reductions in the *M. edax* and *D. minutus* populations in the study lakes were primarily due to decreases in nauplii and early copepodids, but empirical evidence indicating a sensitivity to low pH by these forms is apparently lacking. The decline in phytoplankton abundance may also have contributed to the decline of younger crustaceans, which due to their smaller size had higher metabolic rates and may have greater food requirements than the later stages. Nauplii and early copepodids may also have been at a competitive disadvantage due to lower grazing rates, and lack of sufficient lipid reserves to see them through a period of starvation.

The existence of food limitation is demonstrated by the fact that egg production either ceased or was greatly reduced in most species immediately after liming. This was especially obvious in Cranberry Pond where *D. minutus* had just started to produce eggs. *Diaptomus minutus* resumed egg production in both lakes by July, most likely in response to increasing phytoplankton standing stocks (Bukaveckas 1989).

An additional problem was the presence of relatively large populations of first and second instar *Chaoborus* in both lakes during the immediate postliming period that did not appear to be affected by either neutralization or, initially, the introduction of brook trout (Evans 1989; M. Robbins, Indiana University, pers. comm. (Woods Lake)). These stages are efficient predators (Pastorok 1980), having the potential to contribute to the decline of soft bodied forms such as nauplii and the rotifers *Synchaeta* and *Polyarthra*, the latter two of which are among their preferred prey (Moore and Gilbert 1987). *Chaoborus* appears to eat only negligible amounts of *Keratella* (Fedorenko 1975) so their presence probably had little impact on the *K. taurocephala* populations.

Preliming data from Woods Lake and Cranberry Pond support the contention that *Chaoborus* predation may have had a significant impact on *D. minutus* during the first few weeks following base addition. Data from approximately the same period in 1984 show declines in nauplii which do not appear to be compensated for by increased numbers of copepodids. Losses were greater in Woods Lake than in Cranberry Pond, but the lack of quantitative *Chaoborus* data from the former

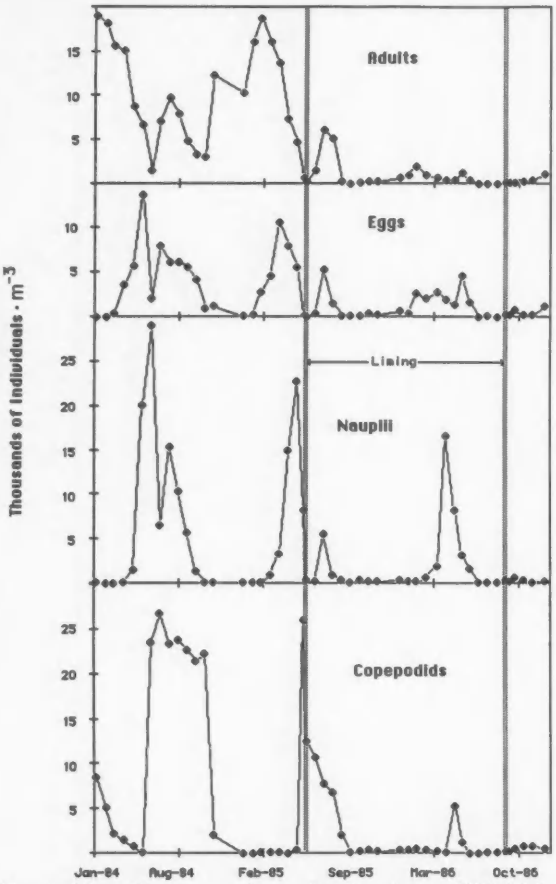


FIG. 6. Mean *Diaptomus minutus* densities during 1984–86 in Woods Lake.

precludes a more detailed analysis. However, if predation was a significant factor in 1984 there was the potential for an even greater impact in Cranberry Pond in 1985 when *C. americanus* was almost twice as abundant (Evans 1989).

The continued decline of *D. minutus* in both lakes during the latter part of 1985 lacks an obvious explanation. The resumption of egg production had only a limited positive effect. Significant predation by *C. americanus* in Cranberry Pond was unlikely as the introduced trout all but eliminated the larvae from the water column (Evans 1989). Brook trout also preyed upon *C. punctipennis* in Woods Lake (Gloss et al. 1989), but what impact this had on the population is not known. The increased egg clutch size in Woods Lake during this period implies that food was adequate for *D. minutus* females, but information is lacking for the other developmental stages. Other possible biological interactions will be considered shortly.

The success of *D. catawba* in Cranberry Pond appeared to be short lived as numbers were considerably reduced in 1986, most likely a consequence of the lake having reacidified. By contrast, the species increased substantially in Woods Lake where the pH had a range of about 6.0–6.5, and a second application of lime in 1986 helped maintain circumneutral conditions (Fordham and Driscoll 1989). Predation by *C. americanus* was unlikely in Cranberry Pond (Evans 1989), but the fact that *C.*

TABLE 6. Woods Lake *Diaptomus minutus* mean egg clutch size and eggs·female$^{-1}$ ratio 1984–86.

| Egg clutch size | Mean | SE |
|---|---|---|
| 1984 Annual | 5.3 | 0.07 |
| Maximum (25 June) | 6.9 | 0.2 |
| Minimum (29 Oct.) | 3.9 | 0.2 |
| 1985 Annual | 5.2 | 0.06 |
| Maximum (28 Oct.) | 11.8 | 1.8 |
| Minimum (28 May) | 1.9 | 0.3 |
| 1986 Annual | 11.6 | 0.2 |
| Maximum (30 June) | 7.0 | 1.0 |
| Minimum (24 Sept.) | 25.0 | 1.0 |
| Eggs·female$^{-1}$ | | |
| 1984 Annual | 1.8 | 0.4 |
| Maximum (14 May) | 4.1 | |
| Minimum (9 Mar.) | 0.09 | |
| 1985 Preliming | 1.7 | 0.6 |
| Maximum (13 May) | 3.4 | |
| Minimum (29 Jan.) | 0.03 | |
| Postliming | 2.5 | 0.5 |
| Maximum (15 July) | 4.2 | |
| Minimum (26 Aug.) | 1.0 | |
| 1986 Annual | 6.7 | 1.0 |
| Maximum (24 Sept.) | 12.5 | |
| Minimum (30 June) | 0.6 | |

*punctipennis* was still present in Woods Lake in 1986 (M. Robbins, Indiana University, pers. comm.), and that *D. catawba* was also subjected to periodic heavy predation by brook trout that year (Gloss et al. 1989) tend to implicate low pH as the primary limiting factor in the former pond.

Unlike *D. catawba*, *B. longirostris* does not appear to be sensitive to lowered pH (Havens and DeCosta 1985), and is commonly found in acidified lakes (Keller and Pitblado 1984). Since the species was abundant in Woods Lake prior to liming, but surprisingly rare in Cranberry Pond, it was almost likely limited by *C. americanus* predation in the latter since *Bosmina* is considered to be an ideal prey species for chaoborids (Pastorok 1980; Reissen et al. 1984). The success of *B. longirostris* in Cranberry Pond in 1986, after possibly being limited by competition with *D. catawba* (Goulden et al. 1982) during the postliming 1985 was most likely due to the decline of *C. americanus*. *Bosmina* was apparently able to compete with *D. minutus* which also responded positively to the elimination of *C. americanus*, but the greatly reduced egg clutch size in *D. minutus* in 1986 versus 1984 and 1985 suggests that food was limiting the zooplankton community. The reduced abundance of *K. taurocepala* lends support to this argument.

The resurgence of *D. minutus* in Cranberry Pond in 1986 was apparently due to the hatching of diapause eggs as few adults and no eggs were observed prior to the appearance of numerous nauplii in April. The production of these eggs, which can rest in the sediments for an extended period before hatching (Hairston and Munns 1984; Hairston and Olds 1984) quite likely evolved to combat seasonally heavy predation by *C. americanus*. A similar response has been reported for *Diaptomus sanquineus* that was preyed upon by sunfish (Hairston and Munns 1984).

The *D. minutus* population in Woods Lake did not appear to produce diapause eggs, and thereby lacked the ability to rapidly recoup losses incurred during the postliming period of 1985. But why the population did not make at least a modest come-

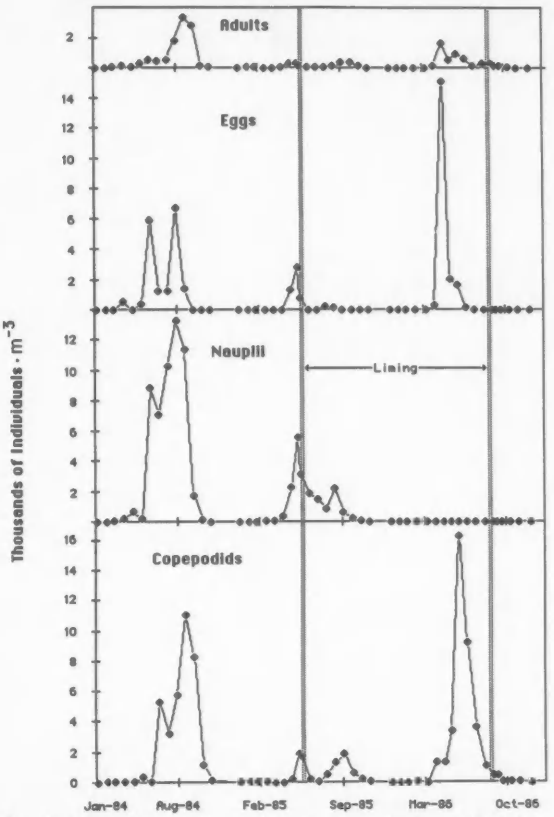


FIG. 7. Mean *Mesocyclops edax* densities during 1984–86 in Woods Lake.

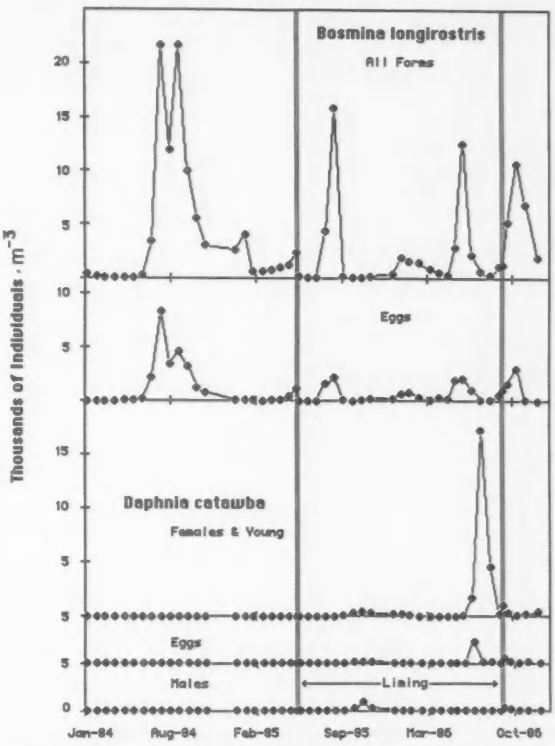


FIG. 8. Mean densities of *Bosmina longirostris* and *Daphnia catawba* during 1984–86 in Woods Lake.

back in 1986 is not clear. Although adults were not numerous, mean egg clutch size was considerably larger than the previous 2 yr. Egg production was continued through the winter of 1985–86, gradually increasing the population, but the eggs and nauplii that were observed through June 1986 yielded few copepodids. It appears that this lack of success was possibly due to the coincidence of several factors. *Chaoborus punctipennis* was still present in the lake (M. Robbins, Indiana University, pers. comm.), and predation by early instars possibly contributed to the apparent naupliar mortality in June and July as was suggested for the previous 2 yr. In Cranberry Pond where the *C. americanus* population was much reduced nauplii and copepodids were not affected. Second, *M. edax* was more abundant in Woods Lake during the early summer of 1986 than it had been the previous 2 yr due to a mid-May egg peak. As a result copepodids, which are known to prey on young diaptomids (Jamison 1980), were numerous during early summer. Similar peaks occurred later in 1984 and 1985. Lastly, the two cladocerans that were abundant later in the summer quite likely increasing the competition for food, especially for the immature stages. Although *B. longirostris* was common prior to liming, *D. catawba*, a highly efficient grazer (Goulden et al. 1982), was below detection prior to the summer of 1985. Singly, any of the above may not have had a serious effect on *D. minutus*, but combined as they were they quite likely had a significant impact on *D. minutus* which was attempting to compensate for losses associated with base addition. Later that year, following the decline in *B. longirostris*, *D. catawba*, and *M. edax*, *D. minutus* again began to increase in number. Food was apparently adequate as the mean egg clutch size was still relatively large, but animal standing stocks were an order of magnitude lower than during the winter of 1985–86 possibly indicating a slow recovery for *D. minutus* in Woods Lake.

The only other crustacean to increase in Woods Lake after neutralization was *C. scutifer* which was rarely observed prior to liming. The species has been reported in other Adirondack lakes (Hall and Waterman 1968), and is commonly found in cold, slightly acidic to near neutral waters (Keller and Pitblado 1984), suggesting that the rise in abundance following base addition may have been due to less acid conditions. Although the slightly cooler water temperatures in 1985 and 1986 may also have enhanced the species' success. Conditions in the lake appeared to remain favorable, as *C. scutifer* was even more numerous in 1987, with many egg-bearing females being noted (W. R. Schaffner, unpubl. data).

A second diaptomid, *D. leptopus* was found only in Cranberry Pond, although the species has been noted in other Adirondack lakes (Hall and Waterman 1968). The increased abundance of the species following liming may have been the result of several factors; a reduced competition for food with *D. minutus*; a relief in population suppression due to less crowded conditions (O'Brien et al. 1973); or a decline in predation by *C. americanus*. But there was also the possibility of opportunistic migration into the pelagic portion of the lake following the decline in *D. minutus*. Movement of this nature from an unsampled region of the lake would result in an increase in prominence but not necessarily numbers of individuals. Data from

early 1986 showing a rapid increase in density of late copepodids and adults in the water column without the presence of earlier developmental stages suggest this type of behavior.

In conclusion, there were obvious changes in the zooplankton commnities of both lakes following base addition and the introduction of brook trout, characterized by a general decline in all taxa shortly after neutralization. Young crustaceans and rotifers appeared to be particularly affected. The reduction in *K. taurocephala* standing stocks had a marked effect on the rotifer communities, as none of the existing taxa were able to replace it in abundance. But the reduction in rotifer densities did necessarily imply a detrimental effect, as *K. taurocephala* dominance is symptomatic of acid stressed systems. A shift towards numerically smaller rotifer communities with more species having shared dominance indicates a trend in the direction of communities more typical of less acidic lakes (Roff and Kwiatkowski 1977).

Longer term changes, primarily the result of biological interactions, were not necessarily the same in each lake. Both communities had previously rare crustacean species increase in abundance, but there were indications of increased competition for limited resources. No new highly acid sensitive species appeared in either lake.

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# Short-Term Changes in the Acid/Base Chemistry of Two Acidic Lakes Following Calcium Carbonate Treatment

G. F. Fordham and C. T. Driscoll

*Department of Civil Engineering, Syracuse University, Syracuse, NY 13244*

Fordham, G. F., and C. T. Driscoll. 1989. Short-term changes in the acid/base chemistry of two acidic lakes following calcium carbonate treatment. Can. J. Fish. Aquat. Sci. 46: 306–314.

Woods Lake and Cranberry Pond, two chronically acidic lakes located in the Adirondack region of New York, USA, were intensively monitored following $CaCO_3$ treatment in May 1985 to evaluate the mechanisms controlling short-term changes in water column chemistry. Immediately following base application (24 h), both lakes responded like systems closed to atmospheric $CO_2$, because the dissolution of very small $CaCO_3$ particles (median diameter 2 μm) exceeded the rate of atmospheric $CO_2$ intrusion. Rapid dissolution of $CaCO_3$ coupled with very low concentrations of dissolved inorganic carbon (DIC) prior to treatment, resulted in pH increases in the upper mixed waters from 4.9 to 9.4 in Woods Lake and from 4.6 to 9.1 in Cranberry Pond, as waters readily became saturated with $CaCO_3$. pH increases were accompanied by stoichiometric increases in dissolved $Ca^{2+}$, acid neutralizing capacity (ANC), and DIC. Following this initial perturbation, the upper mixed waters equilibrated with atmospheric $CO_2$ over a 4 wk period, facilitating additional release of dissolved $Ca^{2+}$ and ANC due to dissolution of suspended $CaCO_3$. The amount of $CaCO_3$ that dissolved during the 4 wk immediately following treatment, calculated from $Ca^{2+}$ budgets, was very high; 86% in Woods Lake and 79% in Cranberry Pond.

Le lac Woods et l'étang Cranberry, deux nappes d'eau acidifiées de façon chronique situées dans la région des Adirondacks, dans l'État de New York (É.-U.), ont fait l'objet d'une surveillance intensive après avoir reçu un traitement au $CaCO_3$ en mai 1985 : on voulait étudier les mécanismes gouvernant les changements à court terme de la chimie de l'eau. On a constaté qu'immédiatement après l'application de la base (24 h), les deux lacs se comportaient comme des systèmes imperméables au $CO_2$ atmosphérique car la dissolution des très petites particules de $CaCO_3$ (diamètre moyen : 2 μm) était plus rapide que la pénétration du $CO_2$ atmosphérique. À cause de la rapidité de la dissolution du $CaCO_3$ et du fait que les concentrations de carbone inorganique dissous (CID) étaient très basses avant le traitement, le pH des eaux mélangées des couches supérieures est passé de 4,9 à 9,4 dans le lac Woods et de 4,6 à 9,1 dans l'étang Cranberry, l'eau s'étant vite saturée en $CaCO_3$. Cette élévation de pH s'est accompagnée d'une augmentation stoechiométrique du $Ca^{2+}$ dissous, de la capacité de neutralisation de l'acide (CNA) et du CID. Après cette perturbation initiale, les eaux mélangées de la couche supérieure se sont rééquilibrées en 4 sem avec le $CO_2$ atmosphérique, de sorte que la libération de $Ca^{2+}$ dissous et la CNA se sont trouvés accrues par la dissolution du $CaCO_3$ en suspension. D'après le calcul des bilans du $Ca^{2+}$, il s'est dissous une quantité très élevée de $CaCO_3$ durant les quatre semaines suivant immédiatement le traitement, soit 86 % dans le lac Woods et 79 % dans l'étang Cranberry.

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There is currently considerable concern over the impact of acidic deposition on surface water quality in Scandinavia and eastern North America (Likens et al. 1979). Atmospheric inputs of strong acids to acid-sensitive regions may contribute to surface water acidification (Johnson 1979; Driscoll and Newton 1985). A variety of water quality problems are associated with this phenomenon, including elevated trace metal concentrations (Baker 1982), increases in lake transparency, and reduction in thermal stability (Yan 1983; Effler et al. 1985), as well as effects on aquatic organisms (Baker et al. 1984).

One technique that has been used to reduce the effects of surface-water acidification is neutralization through treatment with alkaline materials. Various materials such as calcium oxide, calcium hydroxide, calcium carbonate, sodium hydroxide, sodium carbonate, olivine, fly ash, and industrial slags have been used or proposed for use to mitigate the effects of acidification (Grahn and Hultberg 1975).

To date, several studies have been conducted to assess the chemical changes that occur following base application to surface waters. Although important variations have been evident from one study to the next, the general response of surface waters to base treatment has been similar. The immediate consequence of base addition is an increase in pH. The magnitude of the initial pH increase is dependent on the characteristics and concentration of the neutralizing agent used, its method of application, as well as the initial surface-water chemistry. For example, addition of strong bases, such as $Ca(OH)_2$ or NaOH, have resulted in pH increases from 4.8 – 5.2 to 8.5 – 10 (Scheider et al. 1975; Schafran et al. 1982). Although strong bases readily neutralize acidity, rapid increase in pH (pH shock) are generally considered undesirable because of potentially deleterious effects on plankton and fish (Scheider et al. 1975; Baker et al. 1984).

[1]This is part of a series of 13 papers devoted to the Lake Acidification Mitigation Project.

Application of $CaCO_3$ is more widely used for lake neutralization. Addition of a week base coupled with the relatively slow dissolution kinetics of $CaCO_3$ tend to reduce the likelihood of abrupt changes in pH. Although equilibria of $CaCO_3$ in pure water, excluding reactions with atmospheric $CO_2$, can theoretically result in pH values of 9.9 (Stumm and Morgan 1981), the rate of pH increase and final pH value following base treatment depends on the initial chemistry of the surface water, the particle size of the $CaCO_3$, impurities (e.g. Mg) in the $CaCO_3$ and the time of water contact with the $CaCO_3$ (Driscoll and Schafran 1984; Warfvinge et al. 1984). The presence of hydrolyzing metals (e.g. Al and Fe) and dissolved organic carbon (DOC) can also influence the rate and magnitude of pH increase by serving as pH buffers or coating $CaCO_3$ particles, thus curtailing dissolution (Driscoll et al. 1982).

The short-term pH response of lakes treated with $CaCO_3$ has varied among studies reported in the literature. Dillon et al. (1979) indicated initial pH increases between 7 and 8 following $CaCO_3$ addition to a lake in Ontario, Canada. Spreading of $CaCO_3$ onto the ice of two Norwegian lakes resulted in maximum pH values of 6.4 and 7.4 5 d after ice-out (Wright 1985). Driscoll et al. (1982) reported that the maximum pH of 5.6 was not observed until nearly 4 wk after $CaCO_3$ treatment of a Adirondack, New York lake. However, none of these studies involved a detailed evaluation of short-term changes in water chemistry following base application. Only one study has evaluated changes in lake pH over daily time intervals, immediately after $CaCO_3$ addition. Molot et al. (1986) reported modest pH increases for Bowland (whole-lake pH 5.6 – 6.8) and Trout (whole-lake pH 5.9 – 6.4) lakes in Ontario, Canada, with local maximum values greater than 8.0 before adequate mixing occurred.

In addition to increases in pH, increases in water column concentrations of $Ca^{2+}$, ANC, and DIC accompany $CaCO_3$ application. Consequences of base application to surface waters include hydrolysis and deposition of trace metals, as well as changes in DOC concentration (Driscoll et al. 1982; Wright 1985).

Variations in the immediate chemical response of lakes to base treatment, reported in the literature, are undoubtedly due to differences in the initial chemical characteristics and $CaCO_3$ dissolution efficiencies. Factors such as water temperature, initial pH and DIC, the particle size and composition of the $CaCO_3$, as well as the method of base application can greatly affect the rate and magnitude of the initial dissolution (Sverdrup and Bejerle 1983; Driscoll and Schafran 1984; Warfvinge et al. 1984; Molot et al. 1986). Evaluations of the short-term response to base treatment have been hampered by inadequate monitoring of water chemistry immediately following application. Given the biological effects often associated with $CaCO_3$ treatment, a better understanding of the processes regulating short-term changes in water chemistry is needed. Consequently, as part of the Lake Acidification Mitigation Project (LAMP), a study was conducted to evaluate mechanisms controlling the acid/base chemistry of two chronically acidic lakes immediately following application with $CaCO_3$.

## Site Description and Methods

The study lakes, Woods Lake (42°52′N, 71°58′W) and Cranberry Pond (43°51′N, 74°58′W) are located in Herkimer County, New York, in the west-central Adirondack Mountains and are generally typical of chronically acidic lakes in that area (Driscoll and Newton 1985). The watersheds are forested with primarily deciduous vegetation and the surficial geology is generally characterized by thin till (<3m depth). Both lakes are relatively small and shallow, with short hydraulic residence times. A description of the watershed characteristics and hydrology is provided in Staubitz and Zarriello (1989).

Water samples were collected for chemical analyses at the outlets, major inlets, and at several depths from a water column station located at the site of maximum depth in each lake. The water column station was sampled at 0, 1, 2, 4, 6, 8, 10, and 11 m in Woods Lake and at 0, 2, 4, and 6 m in Cranberry Pond. Stations were sampled at approximately 3 wk intervals beginning in January 1984. The water column samples were collected with a 4-L Kemmerer sampler. The samples were collected and stored in a 1-L polyethylene bottle, which had been previously acid washed and rinsed several times with deionized water. A separate aliquot was dispensed into a 60-mL polyethylene bottle devoid of gas head space for DIC and DOC analyses. This collection allowed the DIC sample to remain sealed until the time of analysis in order to minimize gaseous losses or gains.

Following the field activities, solutions were measured for pH at a field station within 24 h of collection. Water chemistry samples were then transported to Syracuse University. Upon arrival, the samples were immediately analyzed for DOC, DIC, $NH_4^+$, $Cl^-$, $NO_3^-$, and $SO_4^{2-}$, generally within 72 h of collection. Samples were stored at 4°C until the remainder of the analyses could be performed (see Table 1), generally within 1 mo after collection. Triplicate samples were taken for a minimum of 5% of the samples collected. Chemical analyses of the triplicate samples were used to estimate a combination of analytical and sampling error. The precision listed in Table 1 for each chemical parameter is an average of the analytical and sampling errors calculated over the length of the study, (January 1984 to September 1985) and is expressed as a coefficient of variation. The precision associated with most of the chemical analyses were generally good (see Table 1). An exception to this trend is the precision associated with ANC and $Cl^-$ determinations. An explanation for the large relative error associated with the measurement of these analysts is that the measured concentrations of $Cl^-$ and ANC (prior to base addition) were low, and therefore even small absolute error between replicates would produce large coefficients of variation.

On 30 and 31 May 1985, 22.6 and 7.2 t (dry mass) of a $CaCO_3$ slurry, with a median particle diameter of 2 μm, were applied by helicopter to Woods Lake and Cranberry Pond, respectively (see Porcella 1989).

An intensive sample collection program was implemented to evaluate lake water chemistry response following $CaCO_3$ addition. Water chemistry samples were collected at the water column and outlet stations on days 1, 2, 6, 10, 20, and 25 following treatment. Shortly after collection (4 h), these samples were measured for pH and an aliquot of the sample was filtered through a 0.1-μm, polycarbonate filter. The filtered sample was analyzed for DIC, DOC, dissolved $Ca^{2+}$, and ANC. Following acid digestion (pH 0.6, 1 h), total $Ca^{2+}$ was analyzed on the remaining unfiltered sample. The difference between total and dissolved $Ca^{2+}$ represents particulate $Ca^{2+}$ and provides an estimate of the undissolved $CaCO_3$ suspended in the water column.

A $Ca^{2+}$ budget was calculated for both lakes to provide a measure of short-term dissolution efficiency obtained from the treatments. The budgets were computed for the period 31 May – 24 June 1985 using stream influx, water column, and lake

TABLE 1. Procedures used in the analysis of lake water samples. Precision represents combined analytical and sampling error obtained from analysis of triplicate samples and expressed as coefficients of variation.

| Parameter | Method | Precision (%) | Reference |
|---|---|---|---|
| pH | Potentiometrically, glass electrode | 0.24 | |
| Acid neutralizing capacity (ANC) | Strong acid titration with Gran plot analysis | 18.0 | Gran 1952 |
| $Ca^{2+}$ | Atomic absorption spectroscopy (AAS) | 2.6 | Slavin 1978 |
| $Mg^{2+}$ | AAS | 2.3 | Slavin 1978 |
| $Na^{+}$ | AAS | 5.6 | Slavin 1978 |
| $K^{+}$ | AAS | 2.4 | Slavin 1978 |
| Dissolved inorganic carbon (DIC) | Syringe stripping of $CO_2$ and detection by gas chromatography | 5.5 | Stainton 1973 |
| $SO_4^{2-}$ | Ion chromatography (IC) | 1.4 | Tabatabai and Dick 1983 |
| $NO_3^{-}$ | IC | 4.9 | Tabatabai and Dick 1983 |
| $Cl^{-}$ | IC | 13.0 | Tabatabi and Dick 1983 |
| Total $F^{-}$ | Potentiometrically with ion selective electrode after TISAB addition | 7.1 | Orion 1976 |
| $NH_4^{+}$ | Phenate colorimetry, autoanalyzer | 5.8 | US EPA 1983 |

efflux data. The amount of $CaCO_3$ dissolved was calculated from the following mass balance:

$$(1)\quad Ca^{2+}_{dissolved} = Ca^{2+}_{final} + Ca^{2+}_{out} - Ca^{2+}_{in} - Ca^{2+}_{initial}$$

where: $Ca^{2+}_{dissolved}$ is $Ca^{2+}$ from the dissolved $CaCO_3$, $Ca^{2+}_{final}$ is $Ca^{2+}$ in the water column on 24 June 1985, $Ca^{2+}_{out}$ is $Ca^{2+}$ exiting the lake through the outlet over the study interval, $Ca^{2+}_{in}$ is $Ca^{2+}$ entering the lake through the inlets over the study interval and $Ca^{2+}_{initial}$ is $Ca^{2+}$ in the water column on 31 May 1985.

Lake volumes used to calculate water column pools of $Ca^{2+}$ were determined from bathymetric maps prepared from surveys completed in July 1984. Hydrologic inflows and outflows were obtained from continuous discharge gauging stations at the lake outlets, operated by the United States Geologic Survey (USGS) (USGS; Staubitz and Zarriello 1989).

A chemical equilibrium model, ALCHEMI (Schecher and Driscoll 1987), was used to calculate theoretical pH, $Ca^{2+}$, ANC, DIC, $H_2CO_3$, $HCO_3^{-}$, $CO_3^{2-}$, and partial pressure of $CO_2$ ($P_{CO_2}$) anticipated following base treatment. Model input included the chemical composition of the lakes prior to treatment, as well as the $Ca^{2+}$ and DIC added from $CaCO_3$ application. Calculations were made both with and without equilibrium with $CaCO_3(s)$, excluding atmospheric $CO_2$ (closed system). A description of numerical procedures and thermodynamic data used in this analysis are summarized in Schecher and Driscoll (1987). To evaluate the proximity of the lake chemistry to equilibrium with $CaCO_3(s)$, mineral saturation indices (*SI*) were calculated

$$(2)\quad SI = \log(Qp/Kp),$$

where: *Qp* is the ion activity product for the lake water and *Kp* is the thermodynamic solubility product for $CaCO_3(s)$ (log *Kp* = 8.38 at 18°C; Stumm and Morgan 1981). Positive, zero, and negative *SI* values suggest conditions of oversaturation, equilibrium, and undersaturation, respectively.

## Results

Prior to base addition, both lakes exhibited pH values below 5, ANC below 0 μeq/L, $Ca^{2+}$ concentrations below 80 μeq/L, and DIC concentrations less than 60 μmol C/L (Fig. 1; Table 2). Before $CaCO_3$ treatment, pH, $Ca^{2+}$ concentrations, and ANC were slightly lower, and DIC concentrations were slightly higher in Cranberry Pond compared with Woods Lake (Table 2). A description of the water chemistry prior to manipulation is available elsewhere (Schofield et al. 1985; Driscoll et al. 1989).

The chemistry of both lakes responded in a similar manner for a 25-d transition period immediately following base application. Because of the similarity in the responses, the results presented here will focus on Woods Lake. Following $CaCO_3$ addition, marked increases in the epilimnetic pH of Woods Lake from 4.9 to 9.5 were observed (Fig. 1a). Coincident with $CaCO_3$ treatment were stoichiometric increases in water column $Ca^{2+}$ and ANC (Fig. 2; $r^2 = 0.987$). However, the complete release of $Ca^{2+}$ and ANC was not achieved instantaneously. Immediately (24 h) following base application, epilimnetic ANC increased from 11 to 218 μeq/L and DIC concentrations increased from 41 to 202 μmol C/L (Fig. 1b and 1d; Table 2). Distinct increases in total $Ca^{2+}$ (from 74 to 780 μeq/L) and dissolved $Ca^{2+}$ (from 74 to 338 μeq/L) were also evident shortly after the manipulation (Fig. 1c). The large discrepancy between total and dissolved $Ca^{2+}$ indicates that elevated concentrations of particulate $CaCO_3$ remained suspended in the epilimnetic waters (Woods Lake 0 – 7 m; Cranberry Pond 0 – 4 m) following the application and dissolution was incomplete.

TABLE 2. Average volume-weighted epilimnetic chemistry for Woods Lake and Cranberry Pond prior to (15 May 1985) and immediately following (31 May 1985) $CaCO_3$ addition. Theoretical concentrations obtained from the model ALCHEMI (water in equilibrium with $CaCO_3$(s) under closed conditions) are also provided for comparison.

| | *Woods Lake* | | | *Cranberry Pond* | | |
|---|---|---|---|---|---|---|
| | Average Pre-treatment Chemistry | Average Post-treatment Chemistry | Results from Theoretical Calculations | Average Pre-treatment Chemistry | Average Post-treatment Chemistry | Results from Theoretical Calculations |
| pH | 4.92 | 9.45 | 9.61 | 4.65 | 9.14 | 9.45 |
| $Ca^{2+}$ (μeq/L) | 74.4 | 338.0 | 370.4 | 67.6 | 374.0 | 416.0 |
| DIC (μmol C/L) | 40.7 | 21202.0 | 189.0 | 58.5 | 236.6 | 232.0 |
| ANC (μeq/L) | −10.8 | 217.6 | 260.0 | −21.7 | 245.0 | 287.0 |
| $HCO_3^-$ (μeq/L) | 1.4 | 177.0 | 160.0 | 1.1 | 220.3 | 206.0 |
| $CO_3^{2-}$ (μeq/L) | — | 49.8 | 58.6 | — | 31.8 | 52.4 |
| *SI* ($CaCO_3$) | | −0.11 | | | −0.26 | |

During the 25-d period immediately following treatment, marked changes in water chemistry were evident as the upper mixed waters reequilibrated with atmospheric $CO_2$. Over this interval, pH values systematically decreased from 9.4 to 7.6, while ANC and DIC increased to values of 450 and 420 μmol C/L, respectively (Fig. 1b and 1d). Shifts in epilimnetic $Ca^{2+}$ were also evident over this transition period, as total $Ca^{2+}$ decreased and dissolved $Ca^{2+}$ increased (Fig. 1c). Within 25 d following base application, particulate $CaCO_3$ was not detected in the water column.

Pronounced changes in the partial pressure of $CO_2$ ($P_{CO_2}$) also occurred due to the perturbation associated with the base treatment (Fig. 1e). Prior to the manipulation, the lake was slightly oversaturated (log $P_{CO_2} = -3.2$) with respect to atmospheric equilibria (log $P_{CO_2} = -3.5$). The $CaCO_3$ application resulted in epilimnetic conditions that were highly undersaturated (log $P_{CO_2} = -5.6$). During the 25-d transition period following treatment, equilibration of the epilimnion with atmospheric $CO_2$ was evident, increasing the $P_{CO_2}$ within the water column. This invasion of $CO_2$ apparently facilitated the dissolution of the remaining suspended $CaCO_3$. The reequilibration was accompanied by a release of dissolved $Ca^{2+}$, ANC, and DIC; along with a decrease to circumneutral pH values expected for a system in equilibrium with atmospheric $CO_2$. For the remainder of the summer period very little change in the pH, ANC, $Ca^{2+}$, and DIC of the epilimnetic waters was evident (Fig. 1).

Although the epilimnion of the study lakes readily responded to base application, treatment effects were generally restricted to these waters. Warm and dry spring conditions facilitated early stratification in both Woods Lake (Fig. 3a) and Cranberry Pond (Fig. 3b). Cranberry Pond is shallow (6.5 m maximum depth) and stratified only slightly, while Woods Lake is deeper (11.5 m maximum depth) and stratified more strongly. Due to conditions of thermal stratification prior to base treatment, the small $CaCO_3$ (median diameter 2 μm) particles were unable to effectively penetrate the thermocline of these lakes. The changes in water chemistry were, therefore, limited to the epilimnetic waters. Within the hypolimnion of Woods Lake, pH values remained below 6, ANC remained below 100 μeq/L and $Ca^{2+}$ continued below 200 μeq/L from the time of $CaCO_3$ application throughout the summer period (Fig. 4). Similar trends were evident in Cranberry Pond, but because it was less strongly stratified than Woods Lake some transport of $CaCO_3$ was apparent throughout the entire water column, resulting in increases in pH and $Ca^{2+}$ in the lower waters (Fig. 5a,b). Fortunately, the volume of untreated water in both lakes was less than 5% of the total lake volume, and thus isolation of this untreated water did not significantly affect the success of the project.

During the 24-h period immediately after application of $CaCO_3$, both lakes approached saturation with respect to the theoretical solubility of $CaCO_3$ for a system closed to atmospheric $CO_2$. Average epilimnetic values of pH, DIC, ANC, and $Ca^{2+}$ for Woods Lake and Cranberry Pond measured following the completion of base application were compared with values calculated using the chemical equilibrium model ALCHEMI, assuming equilibrium with $CaCO_3$(s) (Table 2). These results indicate that both lakes were just slightly undersaturated with respect to the theoretical solubility of $CaCO_3$ following the application. Woods Lake was closer to saturation (*SI* for $CaCO_3$ solubility = −0.11) than Cranberry Pond (*SI* for $CaCO_3$ solubility = −0.26). During the 25-d transition period, as water column pH values decreased, due to inputs of atmospheric $CO_2$, solutions became further undersaturated with respect to $CaCO_3$ (Fig. 1f).

Mass balance calculations for water column $Ca^{2+}$ indicate that the short-term dissolution efficiency of the $CaCO_3$ was very high. For Woods Lake, 86% of the $CaCO_3$ added either dissolved or left the lake through the outlet during the 25-d period following treatment, while the remaining 14% was presumably deposited to the sediments. In Cranberry Pond, over the same period, 79% of the added limestone either dissolved or was flushed from the lake, leaving the remaining 21% deposited within the sediments.

## Discussion

The extremely low DIC concentrations in both lakes, prior to base addition, provided very little buffering against changes in pH following treatment. This low pH buffering, coupled with the low rates of $CO_2$ transfer across the air–water interface, relative to the measurement time scales, caused the lakes to initially respond like systems closed to atmospheric $CO_2$, resulting in pH increases above 9 immediately following $CaCO_3$ addition. The closed system behavior can be attributed to the slurry application of small $CaCO_3$ particles, which created conditions favorable to rapid dissolution (Sverdrup and Bjerle 1983). The settling velocities of the particles were so low that they were unable to effectively penetrate the thermocline effectively. Visual observation confirmed the accumulation of a layer of $CaCO_3$, just above the thermocline. The small $CaCO_3$ particles had a large specific surface area in contact with the water, thus greatly enhancing the rate of dissolution. Lake water rapidly became saturated with $CaCO_3$. Over time, atmospheric $CO_2$

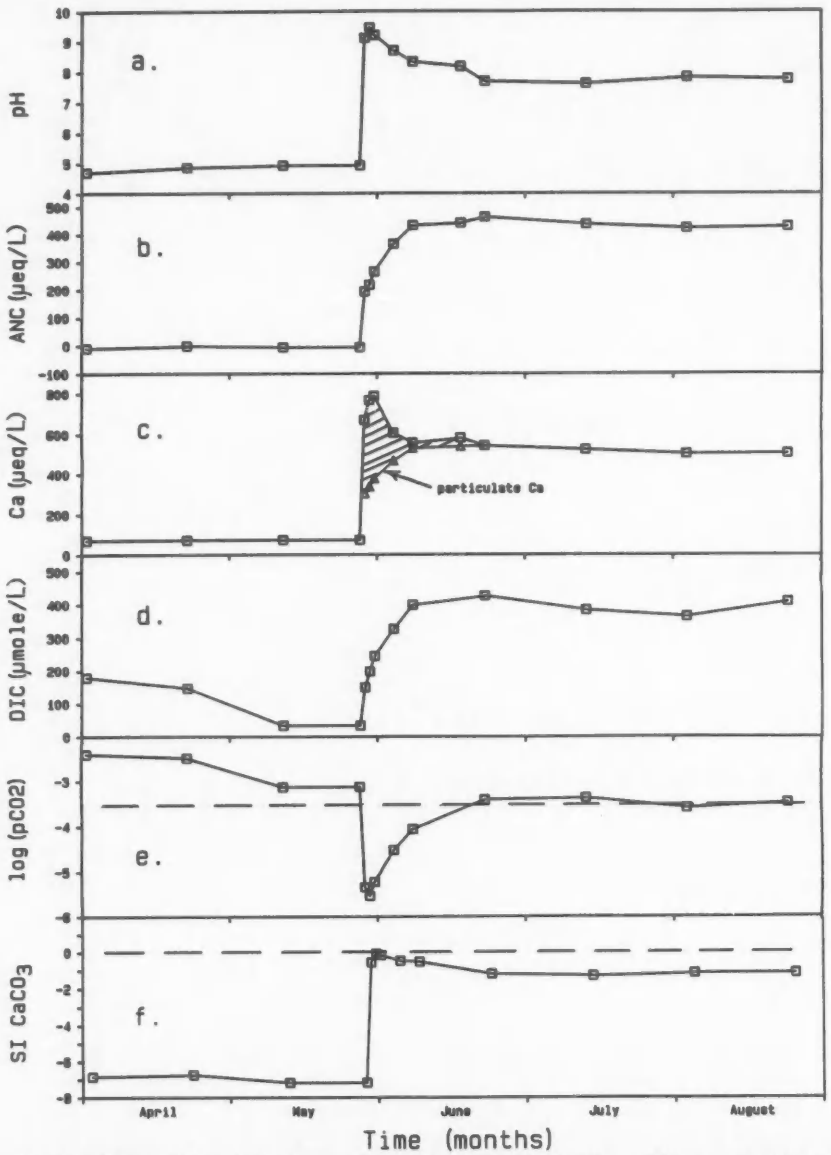


FIG. 1. Epilimnetic (above 6 m) volume-weighted values of (a) pH, (b) acid neutralizing capacity (ANC), (c) total and dissolved $Ca^{2+}$, (d) dissolved inorganic carbon (DIC), (e) the logarithm of the partial pressure of $CO_2$, and (f) *SI* for $CaCO_3$ solubility in Woods Lake prior to and following base treatment (on 30, 31 May 1985).

equilibrated with lake water resulting in conditions of $CaCO_3$ undersaturation and facilitated dissolution of the remaining $CaCO_3$ suspended in the water column. As a result, the dissolution kinetics of the suspended $CaCO_3$ was essentially controlled by the rate of $CO_2$ intrusion into the lake.

Mean epilimnetic pH at Woods Lake just after addition of the $CaCO_3$ (9.45) was slightly higher than at Cranberry Pond (9.14). This difference in pH response between lakes could be attributed to the higher concentrations of DIC present in Cranberry Pond prior to base addition, which more effectively buffered increases in pH.

From water column mass balance calculations, a greater fraction of the $CaCO_3$ added to Woods Lake apparently dissolved during the 25-d period following treatment. Warfvinge et al. (1984) indicated that water column depth is an important factor contributing to the immediate dissolution efficiency of $CaCO_3$ in lakes. The deeper water column and more strongly stratified conditions in Woods Lake appeared to extend the period of particulate $CaCO_3$ suspension relative to Cranberry Pond. As a result, the short-term dissolution efficiency based on water column mass balance calculations was somewhat higher in Woods Lake (86%) compared with Cranberry Pond (79%).

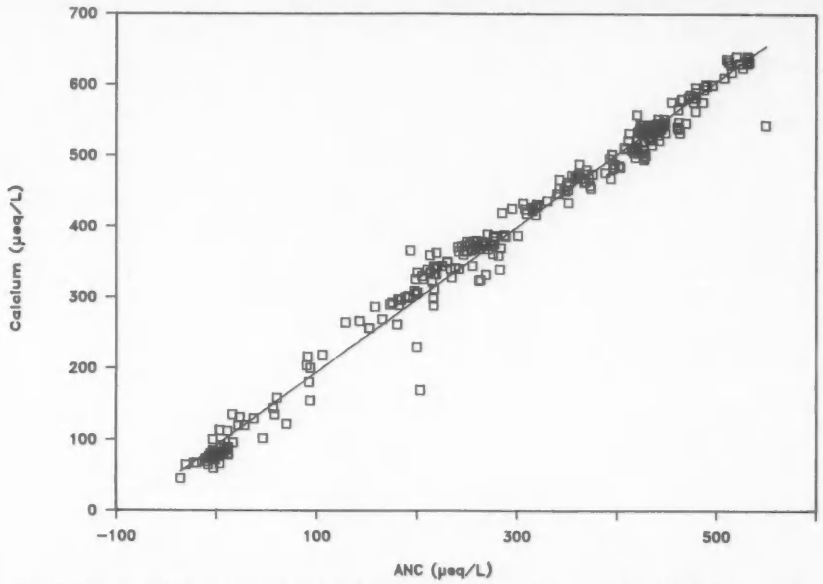


FIG. 2. Dissolved $Ca^{2+}$ concentration as a function of acid neutralizing capacity (ANC) in study lakes. The line is the result of a linear regression analysis.

Our mass balance estimates of deposition of Ca to sediments in Woods Lake (14% of added Ca) were in good agreement with values reported by Young et al. (1989) from sediment Ca measurements 1 mo after treatment (16.8% of added Ca). However, a discrepancy was evident in results obtained using these two approaches for Cranberry Pond (21 versus 5.5% of added Ca). It is difficult to obtain accurate estimates of dissolution efficiency in small, shallow lakes. There are several sources of error associated with both approaches. Uncertainty in water column mass balance calculations may be attributed to a number of factors: error in the actual amount of base added to the lake, error in the determination of volume of small shallow lakes, errors in hydrologic inputs/outputs, as well as analytical error associated with the measurement of water column $Ca^{2+}$. Uncertainty in using changes in sediment pools to assess dissolution efficiency include, heterogenity associated with the deposition of $CaCO_3$ to sediment and uncertainty in recovery of added Ca using sediment extraction procedures. Regardless of the undoubtedly high uncertainty associated with these estimates, both approaches suggest that the dissolution efficiency associated with slurry application of $CaCO_3$ was extremely high.

Previous lake neutralization studies utilizing $CaCO_3$ have not reported the marked increases in pH that we observed. In those studies, it appears that the rate of $CaCO_3$ dissolution was slow enough so that intrusion of atmospheric $CO_2$ was not the rate controlling step in the dissolution kinetics. Moreover, those investigators did not observe the relatively high initial dissolution efficiencies that were evident in our study. In two Norwegian lakes, Wright (1985) reported that only 14% of the applied $CaCO_3$ dissolved within a few days following ice out. Molot et al. (1986) reported 46% dissolution of dry $CaCO_3$ within 2 d of treatment to Bowland Lake. Apparently, higher initial efficiency occurred following slurry $CaCO_3$ treatment of Trout Lake, but unfortunately dissolved Ca measurements were not available to quantify the extent of dissolution. Sverdrup and Bjerle (1983) summarized instantaneous dissolution efficiencies ranging from 17 to 42% for nine lakes treated with $CaCO_3$ in Norway and Sweden. Clearly the small particle size and slurry application greatly facilitated the initial dissolution of $CaCO_3$ in our study.

In future neutralization programs, the abrupt pH increases following $CaCO_3$ addition could be minimized by treating the lakes during periods of high DIC concentrations. Higher DIC concentrations, which have been observed during and immediately following periods of ice cover, would buffer pH changes to within circumneutral values. Moreover, application during unstratified periods would allow for more effective treatment of the entire water column. The application of a larger $CaCO_3$ particle size could also be used to reduce initial pH increase following treatment. Larger sized material has a smaller specific surface area and would more readily penetrate stratified lake water. These conditions would bring about slower dissolution of $CaCO_3$ (Sverdrup and Bjerle 1983). The lake would be less likely to behave as a closed system because the intrusion of atmospheric $CO_2$ into the lake would proceed more rapidly than dissolution of $CaCO_3$. The use of a larger $CaCO_3$ material would reduce the extent of pH increase and a greater percentage would be deposited to the sediments. The long-term dissolution efficiency of $CaCO_3$ deposited to sediments is not well established, and observed responses vary from study to study (Driscoll et al. 1982; Sverdrup and Bjerle 1983; Wright 1985). If sediment $CaCO_3$ dissolution is significant, long-term release of ANC may extend the period before reacidification. However, if $CaCO_3$ deposited to sediments is unreactive then the overall dissolution efficiency would be reduced.

The ecological effects of abrupt changes in water chemistry associated with rapid dissolution of $CaCO_3$ are not well known and represent an important component of the LAMP study. Previous investigators have reported marked reductions of phytoplankton and zooplankton from lakes immediately following base treatment (e.g. Scheider et al. 1975). LAMP researchers

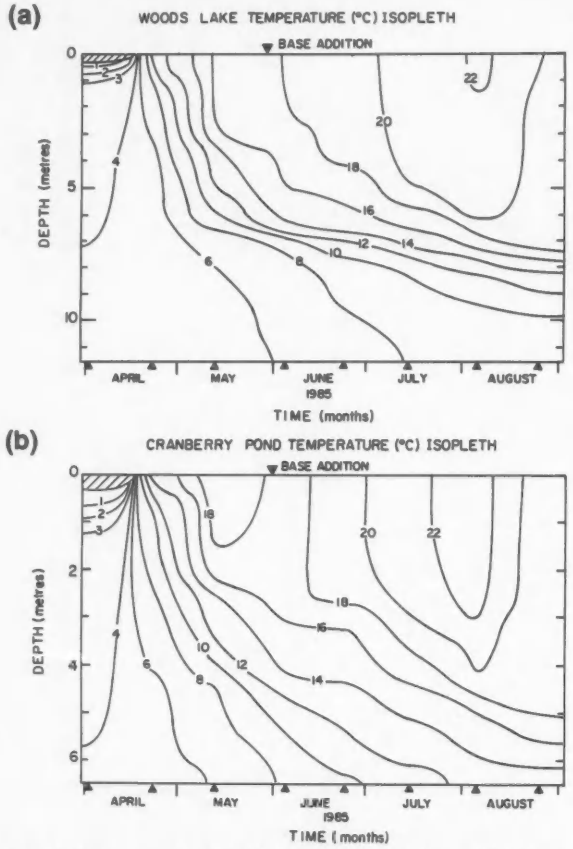


FIG. 3. Temperature isopleth (°C) for (a) Woods Lake and (b) Cranberry Pond prior to and following base addition.

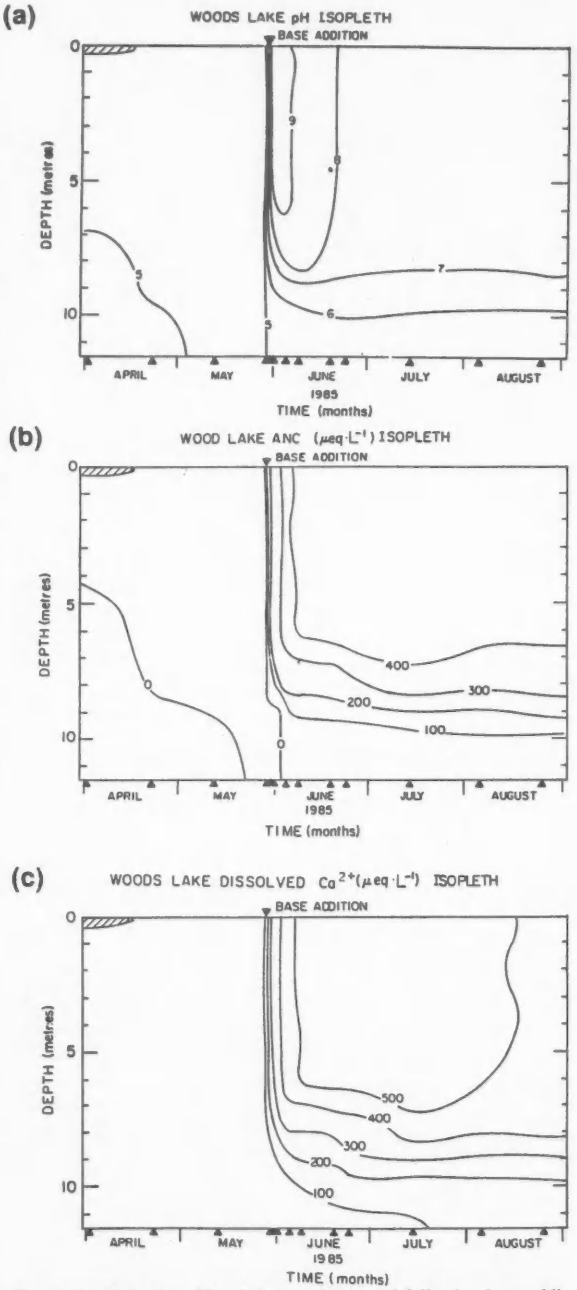


FIG. 4. Isopleths from Woods Lake prior to and following base addition: (a) pH; (b) acid neutralizing capacity (μeq/L); (c) dissolved $Ca^{2+}$ (μeq/L).

have demonstrated similar effects on plankton in Woods Lake and Cranberry Pond. Bukaveckas (1989) observed declines in chlorophyll and phytoplankton biomass shortly after $CaCO_3$ treatment. Schaffner (1989) also reported marked reductions in rotifer and crustacean populations immediately following the manipulation of LAMP lakes. However, Canadian investigators (Yan and Dillon 1981) noted that a small increase in pH or a large increase in pH accomplished gradually, resulted in no change in phytoplankton biomass. The biological effects associated with base treatment appears to be restricted to lower trophic levels. Gloss et al. (1987) observed no detrimental effects of $CaCO_3$ addition on brook trout (*Salvelinus fontinalis*) survival in Woods Lake and Cranberry Pond.

The mechanism(s) responsible for reduction of plankton immediately after base application has not been clearly identified. Possible causes include direct mortality associated with abrupt changes in water chemistry (e.g. pH shock) or physical removal such as cell adsorption onto sinking mineral particles, and/or coagulation with hydrolyzing metals. Bukaveckas (1989) speculated that reduction in phytoplankton growth may be due to $CO_2$ limitations associated with base treatment. Regardless of the mechanism, if the rate and/or extent of water chemistry change is an important factor regulating plankton response to $CaCO_3$ treatment, if may be possible to minimize this perturbation through consideration of water column DIC and $CaCO_3$ particle size.

In summary, several factors must be considered in regulating the short-term response of lakes to neutralization with $CaCO_3$. The chemical and physical characteristics of the lake must be carefully evaluated to select the appropriate base material and

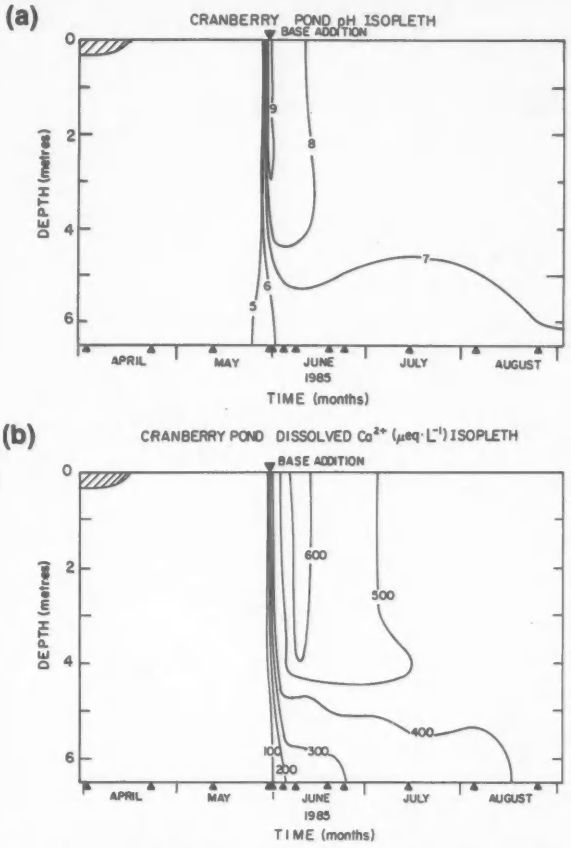


FIG. 5. Isopleths for Cranberry Pond prior to and following base addition: (a) pH; (b) dissolved $Ca^{2+}$ (μeq/L).

method of application for the desired water chemistry response. The correct combination of factors should result in the greatest release of ANC over the longest period for the least cost, while minimizing the perturbation to plankton with the system.

## Acknowledgements

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# Calcite Dose Selection, Treatment Efficiency, and Residual Calcite Fate after Whole-Lake Neutralization[1]

Thomas C. Young[2], Joseph V. DePinto, James R. Rhea, and Richard D. Scheffe[3]

*Department of Civil and Environmental Engineering, W. J. Rowley Laboratories, Clarkson University, Potsdam, NY 13676, USA*

Young, T. C., J. V. DePinto, J. R. Rhea, and R. D. Scheffe. 1989. Calcite dose determination, treatment efficiency, and residual calcite fate after whole-lake neutralization. Can. J. Fish. Aquat. Sci. 46: 315–322.

A modeling approach guided whole-lake neutralization treatments of two acidic Adirondack lakes and aided examination of treatment efficiency as measured by initial water column dissolution and calcite delivery to sediments, prediction of posttreatment water chemistry, and assessment of the fate of calcite deposited on sediments. The lake model incorporated both dissolution and sedimentation of calcite in a vertically segmented lake assumed to behave as a closed system. Observed short-term calcite dissolution exceeded predictions (75 versus 45%) because (1) dispersion and thermocline presence slowed calcite particle settling; and, (2) $CO_2$ influx altered the chemical environment of the particles. Prior to calcite treatment, the two lakes had sediments with similar base neutralizing capacities (BNC). Quantitatively, minor sediment neutralization resulted from the treatment; however, sediment pH gradients changed from positive to negative downward, and $Ca_T$ in surficial sediments increased as sediment BNC decreased. During the subsequent 16 mo of reacidification, sediment chemical characteristics partially returned to pretreatment conditions by contributing alkalinity to the overlying water.

On s'est servi d'un modèle pour élaborer un traitement de neutralisation généralisé appliqué à deux lacs acidifiés des Adirondacks et pour évaluer l'efficacité de l'opération d'après la dissolution initiale dans la colonne d'eau et la pénétration de calcite jusqu'aux sédiments; pour prévoir les caractéristiques chimiques de l'eau après le traitement; et pour examiner ce qu'il advient de la calcite se déposant sur les sédiments. Le modèle représentait la dissolution et la sédimentation de la calcite dans un lac segmenté à la verticale considéré comme un système fermé. La quantité de calcite dissoute à court terme d'après les observations (75 %) a dépassé ce qu'on avait prévu (45 %) parce que : (1) la décantation des particules de calcite a été ralentie à cause de la dispersion et de la thermocline et (2) l'entrée de $CO_2$ a modifié les caractéristiques chimiques dans l'environnement des particules. Avant le traitement à la calcite, les sédiments des deux lacs avaient à peu près la capacité de neutralisation de la base (CNB). Au point de vue quantitatif, le traitement n'a déterminé qu'une neutralisation mineure des sédiments; toutefois, les gradients du pH sédimentaire sont passés du positif au négatif vers le bas et dans les sédiments de surface, le $Ca_t$ a augmenté tandis que la CNB baissait. Durant la réacidification qui s'est opérée au cours des 16 mo suivants, les sédiments ont partiellement retrouvé les caractéristiques chimiques qu'ils avaient avant le traitement en alcalinisant les eaux qui les couvraient.

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Successful neutralization of lake acidity by whole-lake base addition requires several kinds of information: treatment goals for water and sediment, base material requirements, and method of application. A further requirement is an evaluation of treatment effectiveness to guide future mitigation efforts. Selecting treatment goals and determining efficiency can be as straightforward as achievement of a chemical "target." Example targets could be a specified range of posttreatment acid neutralizing capacity (ANC), or neutralization of bottom sediments to a specified depth. Treatment effectiveness may be defined, in turn, by quantifying the correlation between observed effects and chemical targets or other measures predicted from theoretical considerations or ideal conditions.

Estimation of base material requirements, however, is more difficult because dissolution efficiency and the resulting distribution of applied material between water and sediment, depends on several variables (DePinto et al. 1987, 1989). These variables include: (1) properties of the selected neutralization material; (2) method of application; (3) initial water column and sediment acidity to be neutralized (including $CO_2$); (4) final ANC to be achieved, or other treatment "targets"; and, (5) physical features of the lake such as surface area, water depth, stratification, temperature, and hydrodynamics.

Major efforts on the Lake Acidification Mitigation Project (LAMP), described in general by Porcella (1989), concerned selection of treatment materials, estimation of whole-lake neutralization dose requirements, and evaluation of the effectiveness of whole-lake treatment for neutralizing acidic lake water and sediments. Material selection efforts, described elsewhere (Scheffe et al. 1986; Bilz 1986), were limited in scope to calcite-based materials, because these appeared to be most cost effective and efficient for whole-lake applications (Sverdrup and Bjerle 1982; Fraser et al. 1982).

[1]This is part of a series of 13 papers devoted to the Lake Acidification Mitigation Project.

[2]To whom correspondence should be addressed.

[3]Present address: U.S. EPA, EMSL-Research Triangle Park, Research Triangle Park, NC 27711, USA.

In this paper, we report our efforts during LAMP to meet the following objectives: (1) develop and apply a mathematical model for calculation of calcite requirements to achieve target neutralization of the water column and sediments of the two experimental LAMP lakes, Woods Lake and Cranberry Pond; (2) determine the short-term treatment efficiency in terms of initial dissolution in the water column plus delivery to and neutralization of the sediments; and, (3) evaluate the fate of added calcite that does not dissolve, but settles to the sediments. The scope of these efforts was restricted largely to physical and chemical considerations. Related data on LAMP lake locations, watershed characteristics, hydrology, morphometry, and water chemistry changes resulting from calcite addition may be found in other papers in this issue (DePinto et al. 1989, Fordham and Driscoll 1989, Driscoll et al. 1989, Porcella 1989, Staubitz and Zarriello 1989).

## Methods

### Development of Calcite Dose Model

In addition to hydraulic washout, two main factors govern the fate of calcite added to an acidic lake, dissolution and sedimentation. The modeling approach to estimate calcite dose requirements used for LAMP lake treatments gave weight to both of these factors. Calcite was treated as a distribution of particle size classes which, after application to the lake surface, settled through the water column dissolving simultaneously. Dissolution of material in any specific size-class, therefore, resulted in progressively smaller particles during settling and a higher pH environment for dissolution of particles in progressively smaller, slower settling size-classes. A mass balance on the applied calcite permitted prediction of changes in water column chemistry and the amount of calcite that settled to neutralize surficial sediments.

The main assumptions underlying the model appear elsewhere (Scheffe et al. 1986; Scheffe 1987) and will only be summarized here. The lake consisted of several vertical segments through which calcite passed by Stoke's settling. Initially, dispersive fluxes in all directions were assumed negligible compared with sedimentation. Further, the lake was assumed to behave as a closed system with respect to atmospheric $CO_2$ exchange for the short period of calcite settlement. Calcite dissolution kinetics were considered to be controlled by $[H^+]$ and transport at pH <6 and low $CO_2$ partial pressure, and rate-limiting for all modeled acid–base reactions affected by dissolution species (Plummer et al. 1978; Sverdrup et al. 1984; DePinto et al. 1989).

Based on previous work (Plummer et al. 1978; Sverdrup and Bjerle 1982; Bjerle et al. 1982), Scheffe et al. (1986) and Scheffe (1987) developed the expression used in LAMP calculations for the rate of dissolution of calcite in an acidic lake system. The calculation accounted for (1) reaction path dependence on instantaneous pH, $[Ca^{2+}]$, $[H_2CO_3]$, and pH of a calcite saturated solution closed to atmospheric $CO_2$; (2) transport and reaction limitation of dissolution rate, (3) mass of undissolved calcite, (4) diffusion of $H^+$ through the calcite particle boundary layer with a correction for temperature to account for viscosity changes, (5) boundary layer thickness as a function of particle radius, settling velocity, viscosity, and density of water, and density of calcite particles, and (6) temperature-corrected rate coefficients for calcite dissolution and precipitation.

Water chemistry changes during calcite dissolution were tracked by following the transport of each particle size-class through the lake strata, (a user specified number of model segments) to the lake bottom and applying chemical equilibria involving the inorganic carbon and aluminum systems, and dissolved organic carbon (DOC) at each time step. This procedure allowed updating of the water chemistry in a given stratum prior to passage of the next smaller-sized particles. DOC was modeled as a monoprotic acid after the approach of Driscoll et al. (1982). The model contained no fitting parameters; it was entirely deterministic.

Application of the model to the LAMP lakes required specification of pretreatment water chemistry, water depth and surface area, temperature, and areal calcite application rate. The output from the model included time and spatial distributions of ANC, dissolved inorganic carbon (DIC), and pH, water column average values for these quantities, and dissolution efficiency of added material during approach to predicted steady state. Evaluations by Scheffe et al. (1986) and Bilz (1986) demonstrated that the model could accurately predict calcite dissolution efficiencies and resulting chemistry of acidic lake water during neutralizing trials in an undisturbed laboratory column. Additional details on model development and verification may be found in these references.

### Field Program and Sample Analysis

The field sampling and analytical work directly related to the present paper will be mentioned briefly as descriptions of the overall sampling program for LAMP and the study lakes are available in other papers in this issue (Porcella 1989; Driscoll et al. 1989; Staubitz and Zarriello 1989); also, Porcella (1989) has described the calcite treatment logistics for neutralization of the LAMP lakes. Water column samples were collected every 3 wk as part of routine monitoring and intensively (1–7 d collection intervals) around the time of calcite addition. Water column measurements of importance to this paper, on samples collected both routinely and intensively, included: pH (not air-equilibrated), performed potentiometrically (glass electrode) in the field; ANC, DIC, and total and dissolved Ca ($Ca_T$, $Ca^{2+}$), performed in the laboratory, using a strong acid titration and Gran analysis (Gran 1952) for ANC, syringe stripping–gas chromatography detection of $CO_2$ for DIC, and atomic absorption spectroscopy for Ca.

Quantification of calcite treatment effects on sediment-bound acidity (base neutralizing capacity, or BNC) and $Ca_T$ allowed some insight into the extent to which neutralized sediments remained reactive during short-term reacidification, and whether results were consistent with dissolution efficiencies predicted by the dose model and those determined from post-treatment water chemistry.

Sediment samples were collected by gravity coring (Young et al. 1986) before and after calcite treatment (July and August 1984; May, June, September, and October 1985; and September 1986). Because sediments from both lakes were soft (moisture levels generally exceeded 90%), the coring procedure may have resulted in a degree of compaction of sediment solids and smearing of some profiles. Because of the depth integration method used to interpret profiles (described below), compaction did not seriously affect sediment dose estimates. Depth profiles of measured sediment variables, however, may have lost some vertical resolution by the method. Sediment cores were sectioned in the field immediately upon collection at

depths of 2, 4, 6, 8, and 12 cm from the sediment–water interface and stored in whirl-pak plastic bags. The sediment sampling scheme was stratified by depth of overlying water to include spatial variability in estimating calcite requirements for sediment BNC. The depth strata were selected from hypsographic curves of the lakes to divide the surface area into thirds (Woods Lake: <1.5 m, 1.5–3.9 m, >3.9 m) or halves (Cranberry Pond: <1.5m,>1.5m).

Pretreatment estimation of sediment neutralization requirements were obtained from measured vertical profiles of sediment BNC (easily exchangeable acidity; Brown 1943) and sediment bulk density (Page 1982). The product of these quantities, both of which were functions of sediment depth, could be summed incrementally by sediment slice to a specified depth or cumulative mass to estimate calcite equivalents required for sediment neutralization.

Time-dependent changes in the mass of sediment-associated $Ca_T$ and BNC were calculated using an extension of this approach. Area-normalized vertical mass sums of sediment $Ca_T$ and BNC were computed for each sediment sampling period. The pretreatment mass sums provided initial conditions which could be subtracted from those computed from later sampling periods to yield changes in $Ca_T$ and BNC mass accumulations. The pre-, and posttreatment vertical mass sums became essentially linear and usually parallel at depths greater than those affected by the calcite treatment. The depth at which this occurred was selected as the terminal depth for computing the time-dependent changes in sediment accumulation. This computation was applied to each of the water column depth regions used for stratifying the sampling of the lakes. These results subsequently were combined to yield the whole-lake sediment dose estimate when multiplied by the area of each depth region and summed.

Other measured sediment characteristics included moisture content and loss on ignition, both performed according to standard methods of soil analysis (Page 1982), and sediment pH. Sediment pH was measured in the field immediately upon collection by direct insertion of a calibrated combination pH electrode into sediment cores at 2-cm intervals. Because of Donnan potential interferences (Sposito 1984), other procedures may give more accurate pH values. Direct insertion, however, gave consistent, reproducible results and the holding times associated with other procedures that were tested gave rise to variable results.

The results of the sediment characterization were analyzed for differences among and within lakes by analyses of variance (ANOVA) and covariance (ANCOVA). Pretreatment sediment analyses, summarized here, are described more completely elsewhere (Young et al. 1986).

Minor differences existed between lakes in sediment bulk densities when adjusted to constant moisture content (ANCOVA, $0.05 < \alpha < 0.1$). Noted differences resulted from relative sand enrichment of samples from some shallow sites in Woods Lake compared with the predominance of organic matter at most sites in the two systems.

Sediment BNC, as noted by Young et al. (1986), covaried closely with moisture content (ANCOVA, $\alpha < 0.0001$), a relationship that probably reflects the correlation of moisture content with other sediment variables that determine sediment acidity, such as amount of organic matter or hydrous metal oxides. Significant differences did not occur between moisture adjusted lake averages of sediment BNC (ANCOVA, $\alpha > 0.1$), but within each lake BNC depended on the depth of overlying water

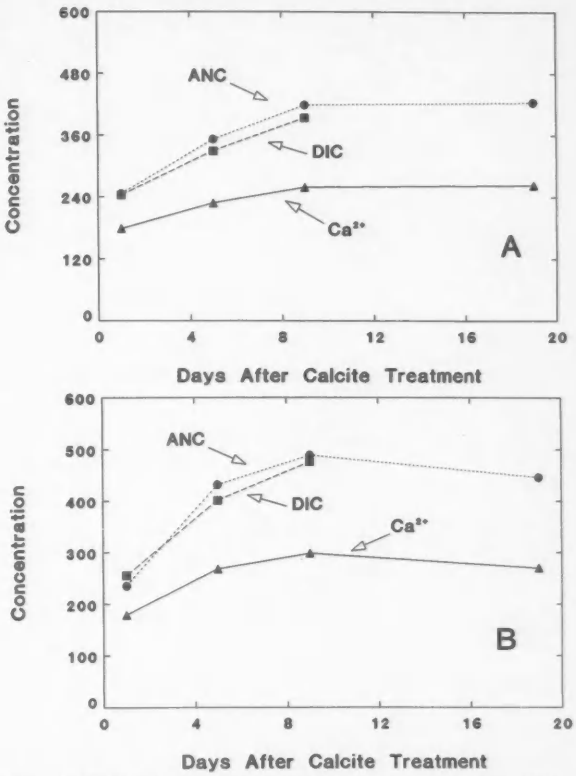


FIG. 1. Whole-lake average transition water chemistry after calcite treatment (DIC, $\mu mol \cdot L^{-1}$, ANC $\mu eq \cdot L^{-1}$, $Ca^{2+}$ $\mu mol \cdot L^{-1}$). (A) Woods Lake, and (B) Cranberry Pond.

(ANCOVA, $\alpha < 0.05$). Shallow water sediments were most acidic in both lakes, possibly due to differences in predominant microbial metabolic activity in the more strongly oxidizing conditions at the sediment–water interface, compared with deep water sediments. Soluble, reduced species (e.g. $Fe^{2+}$, $NH_4^+$, $H_2S$) that form in subsurface sediments as a consequence of microbial activity, subsequently diffuse to the sediment–water interface. Oxidation of these species by molecular oxygen and aerobic microbiota yield $H^+$, which can exchange or adsorb to sediment surfaces at the interface resulting in elevated levels of sediment BNC. Cook et al. (1986), however, found similar rates of $SO_4^{2-}$ reduction ($H_2S$ generation) by sediment microbiota in epilimnetic and hypolimnetic lake regions, suggesting other mechanisms created the dependence of LAMP lake sediment BNC on overlying water depth.

Bulk density and BNC data allowed estimation of calcite requirements to achieve detectable neutralization of sediment in both lakes. The estimates were based on the BNC and bulk density of (1) 2 cm from the top of the 12-cm profile, or (2) 2 cm of core profile average values, and assumed calcite reacted with sediment BNC according to a 1:1 equivalent stoichiometry (Young et al. 1986). Computed in this fashion for 2 cm of profile averaged sediment, sediment calcite requirements for Woods Lake and Cranberry Pond amounted to $5.55 \times 10^3$ kg (22.2 g $CaCO_3 \cdot m^{-2}$) and $1.29 \times 10^3$ kg (17.9 g $CaCO_3 \cdot m^{-2}$), respectively.

TABLE 1. Dose calculation predictions for Woods Lake (dose = 29.6 mg·L$^{-1}$ dry basis) and Cranberry Pond (dose = 34.6 mg·L$^{-1}$ dry basis) based on actual application of Nautex *SL*.

| Description | ANC (μeq·L) | DIC (μm·L) | pH | $Ca^{2+}$ (μeq·L) | Dissolution efficiency (%) | Sediment dose (eq $CaCO_3$·m$^{-2}$) |
|---|---|---|---|---|---|---|
| | | | Woods Lake | | | |
| Pretreatment conditions | −6.7 | 48.8 | 4.88 | 92.2 | | |
| Lake dose model prediction | 248 | 174 | 9.73 | 342 | 44 | 1.12 |
| Open system equilibrium model | 573 | 578 | 8.03 | 672 | 100 | 0.0 |
| Posttransition observations[a] | 420 | 395 | 8.02 | 518 | 73 | 0.54 |
| | | | Cranberry Pond | | | |
| Pretreatment conditions | −15.9 | 72.6 | 4.57 | 80.2 | | |
| Lake dose model prediction | 310 | 237 | 9.60 | 410 | 48 | 1.04 |
| Open system equilibrium model | 662 | 666 | 8.09 | 758 | 100 | 0.0 |
| Posttransition observations[a] | 489 | 477 | 7.40 | 598 | 76 | 0.48 |

[a]Based on water column (whole-lake average) measurements and mass balance on day 9 after treatment.

## Results and Discussion

### Fate of Calcite Addition

Immediately after calcite addition, dramatic increases in pH, DIC, $Ca^{2+}$, and ANC were observed for both lakes (Fordham and Driscoll 1989). Water column pH of both lakes increased from less than 5 to values exceeding 9 within 1 d, and ANC rose from <0 to 420 and 485 μeq·L$^{-1}$ in Woods Lake and Cranberry Pond, respectively, within 9 d of base addition. Approximately equivalent increases in DIC and $Ca^{2+}$ also were observed in the two lakes after treatment.

Based on the pretreatment chemistry and known amounts of calcite applied, the dose calculation model provided predictions, a priori, of the dissolution efficiency and posttreatment water chemistry for both lakes. Observed responses of the two systems during the posttreatment transition period (Fig. 1), compared with the deterministic model predictions, indicate enhanced dissolution of calcite (greater than predicted dissolution efficiency) by the end of the 9 d transition period (Table 1). The predicted dissolution of calcite in Woods Lake was 44% compared with observed dissolution of 73%; these figures for Cranberry Pond were 48 and 76%, respectively.

A comparison of the 9-d calcite dissolution results with data collected 25 d posttreatment indicates as much as 9–13% additional calcite dissolved in Woods Lake (Fordham and Driscoll 1989). In Cranberry Pond, however, no more than 1–3% additional dissolution occurred in the same period. This comparison indicates that the factors leading to enhanced calcite dissolution played a greater role in Woods Lake than in Cranberry Pond.

Calcite dissolution enhancement occurred largely because of model assumption violations involving undisturbed settling and system closure to atmospheric $CO_2$ exchange. The nature of the violated assumptions are reasonably clear from the posttreatment behavior of the neutralized systems. We found undissolved calcite remained in the water column for more than 2 wk after treatment — significantly longer than expected from laboratory settling tests (Bilz 1986). In Woods Lake the delay in settling partly stemmed from the presence of a thermocline, as discussed by Fordham and Driscoll (1989). Because of its shallow character, Cranberry Pond did not display thermal stratification at the time of neutralization. Further, vertical and horizontal hydrodynamic dispersion in the surface waters acted to delay particle settling in both lakes. Scheffe (1987) has tested the sensitivity of calcite dose modeling to vertical dispersion and found the latter to be most significant when very finely divided calcite is applied to lakes as was the case with the LAMP lakes. Finally, the lakes must have experienced significant

TABLE 2. Summary of carbon dioxide influx calculations for Woods Lake (mean depth = 3.49 m) and Cranberry Pond (mean depth = 2.88 m).

| Sampling period | Whole-lake average change[a] DIC | Dissolved calcium | DIC flux[b] | Average surface pH[c] | Average carbon dioxide driving force[a] | $k_L'$ (m·d) | $E^d$ |
|---|---|---|---|---|---|---|---|
| | | | Woods Lake | | | | |
| 6·1–6·5 | 19.8 | 12.8 | 24.43 | 9.04 | 13.0 | 1.88 | 3.42 |
| 6·5–6·9 | 17.8 | 7.4 | 36.30 | 9.17 | 12.98 | 2.80 | 5.09 |
| | | | Cranberry Pond | | | | |
| 6·1–6·5 | 36.5 | 22.5 | 40.32 | 8.86 | 12.47 | 3.23 | 5.87 |
| 6·5–6·9 | 19.0 | 7.38 | 33.47 | 8.75 | 11.30 | 2.96 | 5.38 |

[a](kgmole·m$^{-3}$·d$^{-1}$) × $10^6$.
[b]Atmospheric $CO_2$ intrusion flux in (kgmole C·m$^{-2}$·d$^{-1}$) × $10^6$.
[c]Average between sampling periods.
[d]Assuming $k_L$ = 0.55 m·d$^{-1}$.

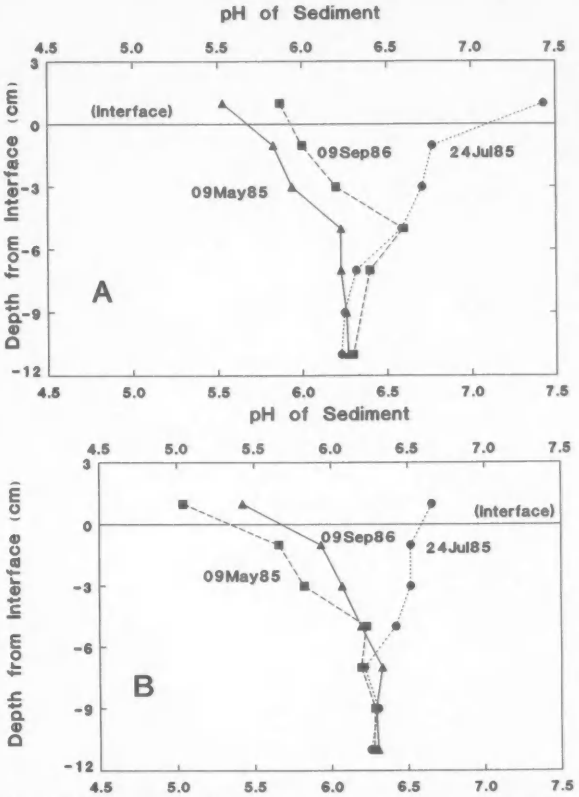


FIG. 2. Sediment pH profiles before and after calcite treatment. (A) Woods Lake, and (B) Cranberry Pond.

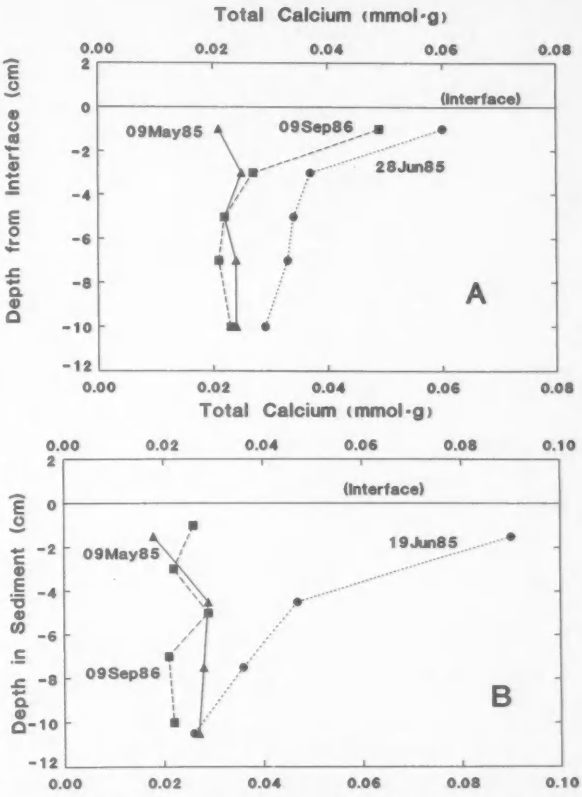


FIG. 3. Sediment $Ca_T$ profiles before and after calcite treatment. (A) Woods Lake, and (B) Cranberry Pond.

influx of $CO_2$ before the calcite settled from the water column to realize the observed ANC and pH levels. The combination of delayed settling and $CO_2$ intrusion resulted in greater than predicted dissolution efficiencies and, consequently, less than predicted sediment neutralization by calcite.

## $CO_2$ Enhancement of Calcite Dissolution

Scheffe (1987) performed a series of sensitivity tests on a more sophisticated version of the present dose model and determined that $CO_2$ exchange (more specifically, the mass transfer coefficient) was the most important factor in enhanced dissolution of calcite. A more thorough examination of this process was undertaken and evaluated using the postneutralization data. During calcite dissolution, in the water column just beneath the air–water interface $CO_2$ can approach 0 and pH may exceed 9. These conditions increase $CO_2$ influx by creating a large $CO_2$ concentration gradient at the interface. This results in a large driving force for $CO_2$ transfer and increases diffusion. A parallel expression of this phenomenon has been reported in lake fertilization studies where algae act as the sink for $CO_2$ rather than calcite (Schindler et al. 1972; Emerson et al. 1973).

In calcite-treated lakes, however, enhanced $CO_2$ transfer can be especially significant because several physical and chemical processes play a role in calcite dissolution. First, the additional $CO_2$ flux will increase lakewater DIC levels and, simultaneously, reduce pH and redistribute inorganic carbon species away from $CO_3^{2-}$. By itself, this mechanism decreases the calcite ion activity product, thereby increasing calcite dissolution capacity. Secondly, the increase in $CO_2$ partial pressure and $[H^+]$ directly enhance dissolution kinetics (Plummer et al. 1978).

Typically, the transfer of $CO_2$ between an air–water interface is modeled with a mass transfer film model (Whitman 1923) in which atmospheric $CO_2$ diffuses through first a gaseous film and then a liquid film (rate controlling for $CO_2$ transport) prior to dispersion in the bulk liquid phase. An underlying assumption in applications of the film model is transport control of the process rate by steady-state diffusion through a uniform stagnant film. Whether this model is physically accurate is debatable; more important is the simplicity of the representation and the fact that the film model yields results almost as accurate as more complex mass transfer models (Dankwerts 1970).

If a film separates the lake surface from the atmosphere, solution of the appropriate diffusion equation for one dimension and no chemical reaction gives

$$R = k_L[CO_{2(eq)} - CO_{2(aq)}];$$

where $R = CO_2$ flux, $k_L$ = true liquid side mass transfer coefficient, $CO_{2(eq)} = CO_2$ at the water surface, $CO_{2(aq)} = CO_2$ at a point away from the surface in the film. If $CO_2$ flux occurs under conditions which lead to reaction (e.g. hydrolysis to $HCO_3^-$), then computation of $R$ involves an apparent mass transfer coefficient ($k_L'$), rather than the true one ($k_L$). To account for this, the enhancement factor for $CO_2$ exchange, $E$, is defined as the ratio of $CO_2$ absorption with chemical reaction

TABLE 3. Response of sediments to whole-lake calcite treatment and subsequent reacidification. (equivalents per square metre).

| | Accumulation of $Ca_T$ | | | Accumulation of BNC | | |
|---|---|---|---|---|---|---|
| | Months after addition | | | Months after addition | | |
| Depth stratum (m) | 1 | 16 | Change over 1–16 mo | 1 | 16 | Change over 1–16 mo |
| | | | Woods Lake | | | |
| < 1.5 | +0.20 | +0.08 | −0.12 | −0.49 | −0.23 | +0.26 |
| 1.5 – 3.9 | +0.36 | +0.12 | −0.24 | −0.31 | −0.14 | +0.17 |
| > 3.9 | +0.26 | +0.03 | −0.23 | −0.34 | −0.28 | +0.06 |
| Average | +0.27 | +0.08 | −0.20 | −0.38 | −0.22 | +0.16 |
| (± SD) | (±0.08) | (±0.04) | (±0.07) | (±0.09) | (±0.07) | (±0.10) |
| | | | Cranberry Pond | | | |
| < 1.5 | +0.06 | +0.01 | −0.05 | −0.08 | −0.13 | −0.05 |
| > 1.5 | +0.20 | 0.00 | −0.20 | −0.12 | −0.17 | −0.05 |
| Average | +0.13 | +0.00 | −0.12 | −0.10 | −0.15 | −0.05 |
| (± SD) | (±0.10) | (±0.01) | (±0.10) | (±0.02) | (±0.03) | (±0.01) |

to absorption without chemical reaction under identical driving forces,

$$R = Ek_L[CO_{2(eq)} - CO_{2(aq)}] = k_L'[CO_{2(eq)} - CO_{2(aq)}].$$

Using a whole-lake approach involving temporal changes in DIC, Scheffe (1987) adjusted for changes in $Ca^{2+}$ and estimated $k_L'$ for the LAMP lakes during the transition dissolution period. The values so computed were converted to enhancement factors ($E$) by dividing each by $k_L$ computed from $CO_2$ diffusivity in pure water and a film thickness of 300 μm (Emerson et al. 1973). Values of $E$ (Table 2) ranged from 3.4–5.9; this magnitude matches that estimated by Emerson et al. (1973) subsequent to fertilizer induced episodes of elevated pH in Lake 227.

The opportunity for enhanced $CO_2$ influx in the treated LAMP lakes arose because the finely divided calcite particles failed to settle without disturbance and as discrete particles. This failure permitted the lakes to act as open systems in violation of assumptions implicit in the dose model. Consequently, depending on water column conditions and the specific acid neutralizing material, prediction of calcite dissolution prior to settling from the water column may require consideration of the effects of $CO_2$ influx during the transition period.

## Fate of Undissolved Calcite

Sediment response to calcite addition may be viewed qualitatively from pH and $Ca_T$ profiles collected approximately a month before, 1–2 mo after, and approximately 16 mo after treatment (Fig. 2A and 2B, Fig. 3A and 3B). The pH profiles plotted in these figures are representative of the responses of the two lakes as demonstrated by the following discussion; however, these data are from individual cores. The Ca data are whole-lake profile averages from depth-stratified samples.

With calcite neutralization, sediment pH in the LAMP lakes followed that of the overlying water near the sediment–water interface and increased from pH 4.8–6.2 before treatment to 6.3–7.2 after treatment. Because the sediment moisture content exceeded 95% of fresh weight in surficial segments (Young et al. 1986) and water column pH changed with treatment from less than 5 to greater than 9 (Fordham and Driscoll 1989), a reversal in the direction of the vertical pH gradient would be expected after treatment. For a period after treatment, therefore, the sediments became a source of BNC to the water column as $H^+$ diffused out and $Ca^{2+}$ diffused into the sediments, along their respective gradients (DePinto et al. 1989).

In contrast, deeper sediment (>6 cm) pH in both lakes generally was poised in the vicinity of 6.2–6.5 and remained unaffected by neutralization of the overlying water. Similar observations near neutral pH poising in subinterfacial sediments have been noted for systems more acidic than the LAMP lakes (Herlihy and Mills 1986). In an experimental whole-lake acidification (Lake 223, Experimental Lakes Area, Ontario), Kelly et al. (1984) found subsurface sediment remained poised at pH ≥ 6.0 after several years of acid addition. Thus, the activity of microflora inhabiting subsurface sediments appears little affected by the acid–base character of overlying water.

A parallel but opposite change in the pH gradient occurred during the posttreatment reacidification period. When reacidification progressed to the point of reducing pH in the overlying water to less than approximately 6.2, the pH gradient assumed its original orientation in the two lakes and sediments once again functioned as sink for $H^+$. These phenomena also are evident in the results of modeling studies by DePinto et al. (1989) of the LAMP and lake neutralization and reacidification processes.

Sediment $Ca_T$ levels showed similar treatment effects in the two lakes, with $Ca_T$ increasing from approximately 0.03 to 0.15 meq·g$^{-1}$ in surface sediments (0–2 cm) immediately after treatment (ANOVA, $\alpha < 0.0001$). Differences were noted in the longer term response of Woods Lake compared with Cranberry Pond. In the latter system the $Ca_T$ gain due to calcite addition largely was lost as reacidification occurred. In Woods Lake, on the other hand, reacidification had not progressed as far as in Cranberry Pond (DePinto et al. 1989), and the data do not indicate the same obvious depletion of sediment $Ca_T$ as in Cranberry Pond (Fig. 3B). These differences were anticipated as Cranberry Pond experienced 7.6 hydraulic residence times (63 d) between the posttreatment sampling periods, compared with 2.8 for Woods Lake (174 d).

Incremental changes in sediment $Ca_T$ and BNC accumulation, computed by the depth–mass summation procedure applied to sediments cored 1 mo before and after and 16 mo after calcite treatment (Table 3), showed unexpectedly weak correlation ($r = -0.521$, $\alpha \approx 0.12$). This resulted from a combination of factors including the relatively small quantity of Ca that entered the sediments, the relatively large spatial variance of sediment BNC, and inaccuracy of the incremental summation procedure as well. Nonetheless, the data suggest exchange of sediment bound $H^+$ for $Ca^{2+}$ occurred as a result of the whole-lake neutralization trials. According to Oliver and Kelso (1983), who reported observations from nearly 100 lakes in north-central Ontario (not treated with calcite), the reverse of this exchange reaction forms an important sediment neutralization reaction during acidification. Laboratory studies and theoretical expectation have led several workers (Sverdrup 1985; Sverdrup and Warfvinge 1985; Scheffe 1987; Scheffe et al. 1986; DePinto et al. 1989) to include a similar $Ca^{2+} - H^+$ ion exchange reaction for modeling acidic lake sediments after calcite neutralization. The LAMP sediment data provide validation from a whole-lake treatment perspective that calcite addition can displace $H^+$ from lake sediment for ion exchange neutralization of future acid inputs.

An approximate value for the total sediment calcite "dose" was computed using data from the 1-mo posttreatment samples (Table 3). Based on changes in depth–mass summations, BNC and $Ca_T$ were expressed as equivalent weights of calcite and averaged, assuming a 1:1 acid–base stoichiometry. Applying this approach indicated the amount of calcite or ANC reaching the sediments of Woods Lake equalled $3.8 \pm 1.1 \times 10^3$ kg $CaCO_3$ ($0.33 \pm 0.10$ eq·m$^{-2}$); for Cranberry Pond the amount was $0.40 \pm 0.22 \times 10^3$ kg $CaCO_3$ ($0.11 \pm 0.06$ eq·m$^{-2}$). These represent quite low levels of sediment treatment. Compared with the total amount of calcite applied, the sediment analysis indicates 16.8 and 5.5% reached the sediments for the two lakes, respectively. Further, these treatment levels fall short of sediment dosages estimated from posttreatment water column chemistry (Table 1), and somewhat less than the estimated calcite requirements for complete neutralization of 2 cm of sediment.

Few data have been published on Ca or ANC accumulation by sediments after whole-lake calcite treatment for comparison with these values. Molot (1986) and Molot et al. (1986) found no increase in Ca content in the top 5 cm of sediments from either Bowland or Trout Lake (Ontario) after lake-wide calcite additions (1.65 and 0.45 eq·m$^{-2}$) that indicated, by mass balance, approximately 0.66 and 0.18 eq $CaCO_3$·m$^{-2}$, respectively, reached the sediments. Future workers may find direct measurements of sediment neutralization generally underestimate mass balance calculation results.

Applying the same procedure to sediments collected 16 mo after calcite addition showed loss of a substantial portion of the treatment-induced sediment ANC during reacidification. Based on changes in cumulative sediment BNC and $Ca_T$, approximately 0.81 and 0.035 eq $CaCO_3$·m$^{-2}$ was lost from Woods Lake and Cranberry Pond sediment during the reacidification period. These data are consistent with the reversible $H^+ - Ca^{2+}$ exchange reactions indicated earlier and suggest the sediment ANC reserve that was created during calcite addition can function as an ANC buffer when acid influx occurs after treatment.

The degree of sediment neutralization achieved and the contribution of sediment-bound ANC to the overlying water column during subsequent reacidification would not be considered a major effect of the LAMP whole-lake treatments performed in May 1985. Preneutralization alkalinity fluxes, due to microbially induced formation of reduced soluble species, ranged from 0.1 to 0.3 eq·m$^{-2}$·yr$^{-1}$, based on mass balances for the two lakes (DePinto et al. 1989; Driscoll et al. 1989). These annual values compare favorably with the summer rates of denitrification and sulfate reduction observed by Rudd et al. (1986) in Woods Lake and substantially exceed the posttreatment fluxes of sediment-bound ANC as defined chemically and presented in the preceeding discussion (0.03–0.14 eq·m$^{-2}$·yr$^{-1}$).

For mitigating acidic conditions in the two lakes, the practical consequence of the sediment neutralization was a minor and short lived postponement of reacidification (DePinto et al. 1989). Nonetheless, the LAMP sediment data do demonstrate continued reactivity during lake reacidification despite the low level of sediment treatment achieved. The extent to which neutralized sediments can continue to release ANC, the effect on reactivity of higher sediment application rates, resolution of chemical mechanisms active in the sediment ANC–BNC reactions, and the response of sediment microflora to calcite addition are areas for ongoing and future research involving mitigation of lake acidity. Ongoing acid lake neutralization activities associated with LAMP will address some of these questions (Porcella 1989).

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# Predicting Reacidification of Calcite Treated Acid Lakes[1]

Joseph V. DePinto[2], Richard D. Scheffe[3], William G. Booty, and Thomas C. Young

*Department of Civil and Environmental Engineering, Clarkson University, Potsdam, NY 13676, USA*

DePinto, J. V., R. D. Scheffe, W. G. Booty, and T. C. Young. 1989. Predicting reacidification of calcite treated acid lakes. Can. J. Fish. Aquat. Sci. 46: 323–332.

A mathematical model (acid lake reacidification model, ALaRM) for predicting reacidification times of calcite treated acid lakes has been calibrated and field tested using data from two Lake Acidification Mitigation Project (LAMP) lakes (Woods Lake and Cranberry Pond, Big Moose, N.Y.) The model is based on dynamic water column and sediment mass balances of acid neutralizing capacity (ANC) and dissolved inorganic carbon (DIC). Inclusion of a sediment submodel that includes sediment–pore water proton exchange, production of DIC through sediment respiration, ANC generation or utilization through redox reactions, long-term dissolution of calcite deposited in the surface sediments during application, and pH adjustment through an equilibrium proton balance, permits the deterministic simulation of sediment response to whole-lake liming and its subsequent effect on water column reacidification. Application of ALaRM to the postliming response of the two lakes demonstrated that reacidification was controlled primarily by hydrologic flushing and secondarily by sediment–water ANC transfer. Cranberry Pond, which has a mean hydraulic retention time of 2 mo, reacidified to near 0 ANC and pH < 5 within 6 mo after treatment. Woods Lake, which has a mean hydraulic retention time of almost 6 mo, still had an ANC > 20 $\mu eq \cdot L^{-1}$ and a pH > 5.6 just prior to its reliming 15 mo after its initial treatment.

Un modèle mathématique (modèle de réacidification, ALaRM) servant à prévoir la durée de la réacidification de lacs traités à la calcite a été étalonné et mis à l'essai avec des données portant sur deux lacs (le lac Woods et l'étang Cranberry, dans l'État de New York) étudiés dans le cadre d'un projet consacré à l'acidification (*Lake Acidification Mitigation Project* (LAMP)). Ce modèle est basé sur les bilans de masse des substances à capacité de neutralisation de l'acide (CNA) et du carbone inorganique dissous (CID) dans la colonne d'eau et dans les sédiments en conditions dynamiques. Pour être en mesure de stimuler de façon déterministe la réaction des sédiments à un traitement généralisé et ses effets sur la réacidification de la colonne d'eau, on a élaboré un sous-modèle mettant en jeu les échanges protoniques dans l'eau des pores sédimentaires, la production de CID due à la respiration sédimentaire, la production ou la consommation de substances à CNA par réactions d'oxydo-réduction, la dissolution à long terme de la calcite déposée à la surface des sédiments durant le traitement et l'ajustement du pH par instauration d'un équilibre protonique. L'application du modèle ALaRM à deux lacs traités à la calcite a permis de constater que la réacidification dépend principalement de l'effet de chasse hydrologique et, de façon secondaire, du transfert de substances à CNA entre les sédiments et l'eau. L'étang Cranberry, dont la rétention hydraulique moyenne est de 2 mo, était réacidifié au bout de 6 mo, la CNA étant presque revenue à 0 et le pH à une valeur inférieure à 5. Le lac Woods, dont la rétention hydraulique atteint presque 6 mo, avait encore une CNA de plus de 20 $\mu eq \cdot L^{-1}$ et un pH de plus de 5,6 juste avant qu'on le traite à nouveau, 15 mo après le traitement initial.

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For both research and management reasons it is desirable to make a prediction of the reacidification time for acid lake systems that have been neutralized by the addition of a base material to the lake's water column. From a research perspective a great deal can be learned about the relative significance of the various processes that led to the original acidification. From a management perspective reacidification modeling is useful for addressing two whole-lake liming questions: (1) what is the feasibility of restoring or preventing further deterioration of a candidate lake? and (2) what is the time schedule for reapplication in order to maintain chemical conditions conducive to a healthy biological community? Additionally, a reacidification model could be used to optimize the treatment scheme for a given lake, because the efficiency of any treatment scheme is coupled to reacidification time. This optimization manifests itself in the possible trade-offs between the factors that govern short-term dissolution efficiency (Young et al. 1989) and the duration of a given treatment.

The need for using a deterministic modeling approach for understanding lake reacidification has been recognized in other whole-lake liming studies in Scandinavia and Canada (Dillon and Scheider 1984; Sverdrup et al. 1984; Sverdrup and Warfvinge 1985; Wright 1985; and Sverdrup 1986). In conjunction with the Electric Power Research Institute (EPRI)-funded Lake Acidification Mitigation Project (LAMP) a mathematical model (acid lake reacidification model, ALaRM) for predicting the reacidification of calcite treated acid lakes has been developed and applied to the postliming period of two lakes (Woods Lake and Cranberry Pond), located in the Adirondack Park of New York. A general overview of the LAMP and description of the

[1]This is part of a series of 13 papers devoted to the Lake Acidification Mitigation Project.

[2]To whom correspondence should be addressed.

[3]Present address: U.S. EPA, EMSL-Research Triangle Park, Research Triangle Park, NC 27711, USA.

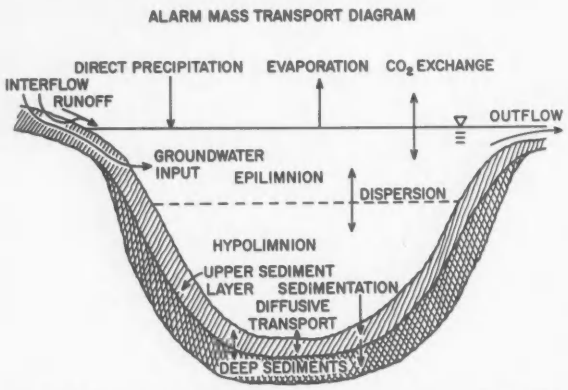


FIG. 1. Diagram of segmentation and mass transport pathways for ALaRM.

lakes and their treatment in May 1985 can be found in Porcella (1989).

The purpose of this paper is to present the development, calibration, and field testing of ALaRM using the data from the two LAMP study lakes for the period of January 1, 1984 through August 31, 1986. The model calibration used the preliming data (January 1984 – May 1985), field testing of the model was performed by making a comparison of its postaudit simulations with the actual reacidification chemical observations for the period of June 1985 through August 1986. Finally, the confirmed model has been applied to illustrate the relative importance and seasonality of factors affecting reacidification.

## Model Development

ALaRM is a general mass balance model designed for the temporal prediction of the principal chemical species in both the water column and sediment–pore water of neutralized water bodies. The model treats reacidification (simulation after addition of neutralizing material) as a dynamic event resulting from a combination of relevant hydrological, chemical, and biochemical processes. The model thus forms a framework for both hypothesis formulation and testing. Model development is based on the assumption that the most useful constituent for defining reacidification is acid neutralizing capacity (ANC). Therefore, the model design and the discussion that follows emphasize the principal processes affecting in-lake ANC. Also, calcium is treated as a state-variable because of its potential significance in fish response (Brown 1983).

In ALaRM the lake and its bottom sediments are partitioned into five segments (Fig. 1). The water column is divided into two layers, based on thermal stratification, an epilimnion (segment 1) and a hypolimnion (segment 2). The bottom sediments are divided into three segments. An active sediment layer (3 cm thick) adjacent to the water column comprises segments 3 and 4; the active sediment layer has been segmented horizontally into segments 3 and 4 based on the sediment surface area fraction exposed to the epilimnion at the time of treatment because of the difference in sediment dosing above and below the thermocline. Finally, a deep sediment layer (segment 5; 9 cm thick) underlies both segments 3 and 4. Also shown in Fig. 1 are the various transboundary mass transfer processes that are included in the model.

Shown in Fig. 2 are schematic diagrams of the water column and sediment transformations that are included in ALaRM. Input loadings of (dissolved inorganic carbon) DIC, ANC, and dissolved calcium are introduced into the epilimnion. These three variables are free from thermodynamic constraints and are treated as time-dependent state variables in all segments. The remaining state variables in the sediment segments include undissolved calcite and total sediment proton exchange sites.

Within each segment time-dependent mass balance equations have been developed for each state variable, based on the conceptualization of transport (Fig. 1) and transformations (Fig. 2). The mass balance equations, in general, include terms for direct loadings, fluxes of species across segment interfaces and system boundaries, biochemical forcing functions, sedimentation, and dissolution of calcite in the sediments. For a particular segment, $j$, a mass balance on the concentration of the $i$th constituent, $C_{ij}$, is summarized by the following equation:

$$(1)\quad V_j \cdot dC_{ij}/dt = W_i(t) + A_{jm} \cdot k_{jm} \cdot (C_{im} - C_{ij}) - Q \cdot C_{ij} \pm GEN(t) + DISS(t) \pm SED(t)$$

where, $V_j$ = volume of segment $j$, $A_{jm}$ = interfacial area between segments $j$ and $m$, $k_{jm}$ = mass transfer coefficient

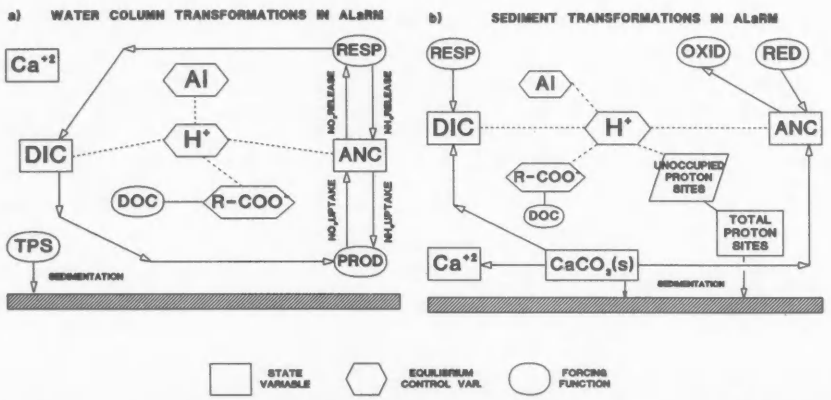


FIG. 2. Conceptual model of (a) water column and (b) sediment transformation pathways for ALaRM. Diagrams show model state variables, forcing functions, and parameters that enter into the equilibrium calculation of pH after each model time step.

across boundary between segments $j$ and $m$, $W_i(t)$ = watershed loading (epilimnetic segment only), $Q$ = outflow from lake (epilimnetic segment only), $GEN(t)$ = internal generation or depletion, due to biochemical transformations, $SED(t)$ = gain or loss through sedimentation mass transport across upper or lower segment boundary, $DISS(t)$ = gain through calcite dissolution in sediment segments.

With three water column segment state variables and five sediment segment state variables, application of equation (1) to the conceptual model produces a system of 21 coupled, first-order, ordinary differential equations. This system of equations is solved via a fourth-order Runge–Kutta algorithm using a half-day time step. After each time step, hydrogen ion, carbonate and monomeric aluminum hydrolysis species concentrations in each segment are updated via a chemical equilibrium routine that incorporates the new values for ANC and DIC with solubility-determined values for aluminum species and a constant forcing concentration of (dissolved organic carbon) DOC. Within the sediments, an additional component for sediment proton-binding sites is included in the proton balance (DePinto et al. 1987).

With respect to internal sources or sinks for DIC and ANC (the *GEN* terms in equation (1)) the model mass balance equations include net biochemical forcing functions for the water column and the sediments segments. In the interest of simplicity and use of the model for management purposes treatment of the internal generation/loss of DIC and ANC as seasonally-adjusted zero-order forcing functions permits a component analysis without the added complexity of explicit modeling of each specific process. The specific processes could be added to the model framework at a later date, if necessary, at the expense of adding state variables for the individual process rate-limiting species. In a broader context, one can interpret the overall dynamic mass balance as providing a framework for quantifying these processes.

In the water column, photosynthesis and respiration are coupled processes that have the most potential influence on model state variables (Schnoor and Stumm 1985; Brezonik et al. 1987). Evidence exists for net alkalinity production due to photosynthesis during the summer growing season in softwater lakes (Bukaveckas 1989; Morgan 1985; Collins et al. 1983); the alkalinity increase generated by net photosynthesis depends largely on the relative assimilation of $NO_3^-$ and $NO_2^-$ versus $NH_4^+$ during the process.

In the sediments the major processes affecting DIC and ANC seem to be respiration, dissimilatory sulfate reduction coupled with iron sulfide formation, denitrification, ammonium production from deamination of organic matter, cation exchange, and sulfate adsorption (Hongve 1978, Oliver and Kelso 1983; Baker et al. 1985; Schindler et al. 1986; and Cook et al. 1986). Although there is a certain seasonal variability, in general the net effect of these processes is to produce ANC and DIC in sediments. This has the effect of causing a quantitatively significant alkalinity flux from the sediments of acid lakes (Carignon 1985). Although water column neutralization of acid lakes may not significantly alter the rate of sediment ANC generation, it most certainly will alter the sediment-water ANC gradient and, thus, the sediment to water flux. Because ALaRM separates the biochemical generation of ANC from the sediment-water transport of species contributing to ANC, it has the capability to differentiate the temporal impact of sediment ANC generation on the water column through the reacidification process.

In addition to the various model coefficients and forcing functions, input data for ALaRM include: lake morphometric characteristics; time-variable hydrologic budget and input loadings; and initial conditions for all concentrations. Morphometric characteristics of the study lakes are presented in Staubitz and Zarriello (1989); water column segment volumes and inter-segment areas were adjusted seasonally to reflect variation in thermal stratification. Initial conditions were established on the basis of field observation, and represent the water column and sediment chemical conditions at the end of the postliming transition period (Young et al. 1989; Fordham and Driscoll 1989).

The time-variable hydrology and principal state variable (DIC, ANC, Ca) loadings that are necessary inputs to ALaRM were obtained from the application of the Watershed Acidification Model (WAM) to the study lakes. WAM is a deterministic model which, based on meteorological and precipitation chemistry inputs, is capable of simulating the hydrologic flowpaths and chemical constituent transport and transformations through a lake's drainage basin (Booty 1983; Booty and Kramer 1984). WAM was calibrated using Woods Lake data from the ILWAS project and confirmed with Woods Lake and Cranberry Pond data from LAMP (Booty et al. 1987).

## ALaRM Calibration/Confirmation

### Model Calibration

ALaRM was calibrated using the Woods Lake pretreatment observations from January 1, 1984 through May 1985. The methodology for quantifying the various kinetic coefficients and forcing terms in ALaRM used a combination of calibration to Woods Lake preliming observations, process experimentation results from this project and the literature, and a rational application of limnological principles.

Some confidence in the model framework was derived from the calibration process in that the model was able to capture the timing and magnitude of significant ANC and DIC fluctuations in the system (Fig. 3). Even when the epilimnion (segment 1) and hypolimnion (segment 2) model simulations were compared separately with volume-weighted data for each segment (Fig. 4), a very close comparison was obtained. This provided confidence in the defined stratification, vertical mixing rates, and sediment-water exchange rates.

Figures 3 and 4 demonstrate several seasonal ANC and DIC fluctuations that are typical of acidic Adirondack drainage lakes such as Woods Lake, namely:

- a mid-winter (February 1984) thaw (Booty et al. 1987; Driscoll et al. 1989) introduced considerable acid into a shallow surface layer of water under the ice, thus causing an epilimnetic ANC depression without significantly influencing the bottom waters;
- sediment reduction processes through the winter that, via sediment-water exchange, increased ANC considerably in the bottom waters;
- sediment decomposition processes that produce $CO_2$ caused a considerable increase in DIC during the ice cover period, because of the greatly reduced atmospheric exchange at this time;
- a major spring acid loading (generally about half the annual load), in combination with the mixing of the stratified layers after ice-off, caused a significant decrease in water column ANC; DIC also dropped rapidly during this period due to dilution and, primarily, atmospheric $CO_2$ exchange;

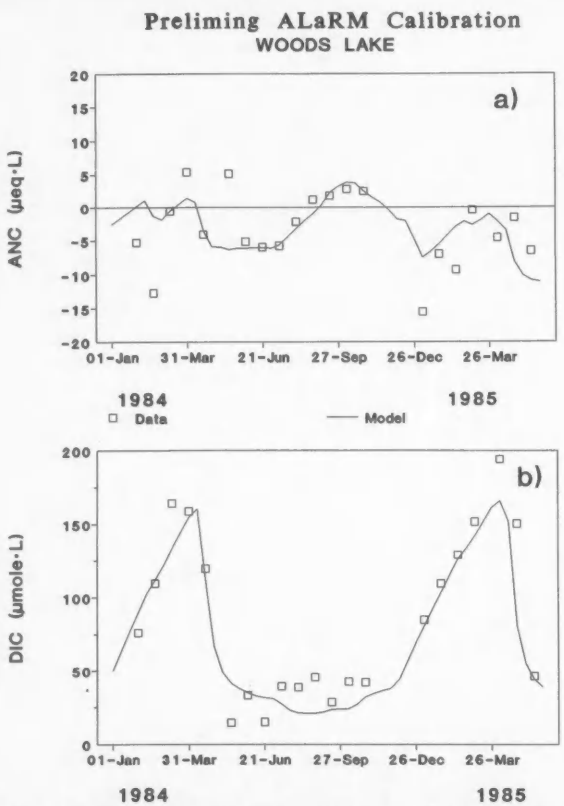


FIG. 3. Results of calibration of ALaRM for the principle state variables (a) water column ANC and (b) water column DIC. Plots show comparison of model output and field observations of whole-lake volume-averaged concentrations for the preliming period.

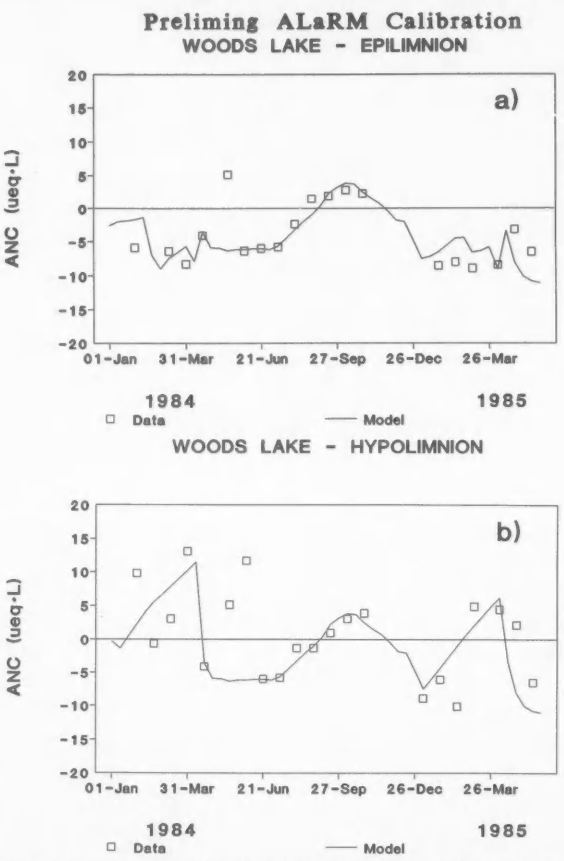


FIG. 4. Results of ALaRM calibration water column ANC in (a) epilimnion (segment 1) and (b) hypolimnion (segment 2). Plots show comparison of model output and field observations of segment-averaged concentrations for the preliming period.

— a gradual increase of ANC through the summer due to higher ANC loading, particularly from the subsurface component, and to the net primary production at this time, which depleted nitrate and kept DIC very low.

The coefficients and forcing functions that produced the calibration of ALaRM shown in Fig. 3 and 4 are summarized in Table 1. The mass transfer coefficients between the various segments of the lake and between segment 1 and the atmosphere ($k_{01}$) are consistent with limnological observations and accepted values for small lakes and ponds (Mortimer 1974; Snodgrass and O'Melia 1975; Snow and DiGiano 1976; DiToro and Connolly 1980; Stumm and Morgan 1981; and Chapra and Reckow 1983). A more detailed discussion of the calibration process can be found in Scheffe (1987).

## Sediment Calcite Dissolution

Sediments can act as either a source or sink for ANC (relative to the water column) through a combination of sediment processes that generate or utilize ANC and mass transfer of chemical species across the sediment-water interface. The sediment submodel of ALaRM (Fig. 2) provides for ANC and DIC generation/utilization and for calcite dissolution and deactivation. At this point in the model development process sediment respiration and redox processes are calibrated as seasonally constant forcing terms, mainly to investigate their significance in reacidification rates. Parameterization of the proton-exchange process was accomplished by titration experiments using Woods Lake and Cranberry Pond bottom sediments as presented in DePinto et al. 1987).

The process of calcite dissolution in water has been thoroughly investigated; it depends on temperature, pH, $CO_2$ partial pressure, extent of saturation, type of material, and local hydrodynamics (Berner and Wilde 1972; Berner and Morse 1974; Plummer et al. 1979; Bjerle et al. 1982; and Sverdrup and Bjerle 1982). The rate of calcite dissolution within lake sediments, however, is complicated by calcite burial and surface deactivation. Both of these mechanisms inhibit the effective neutralization of overlying water by calcite dissolution. Sverdrup et al. (1984) accounted for this inhibition by assigning an empirical, exponential decrease in the dissolution rate constant. ALaRM contains no empirical deactivation term but assumes that undissolved calcite deposited on the sediments is rapidly mixed within the upper, active sediment layer. Dissolution of this deposited calcite is then controlled by pore-water chemistry, not overlying water chemistry, and, in turn, by the sediment processes that affect pore water chemistry. For example, because sediment pore water pH values are well buffered by ion exchange processes (DePinto et al. 1987; Young et al.

TABLE 1. List of values for various ALaRM parameters used during calibration and reacidification runs.

| | | |
|---|---|---|
| **Rate Coefficients ($m \cdot d^{-1}$)** | | |
| Atmospheric exchange rate | ($k_{01}$) | 0.3 |
| Sediment-water mass transfer rate | ($k_{13}$,$k_{14}$,$k_{23}$,$k_{24}$) | 0.01 |
| Upper-lower sediment bound mass transfer | ($k_{35}$,$k_{45}$) | 0.005 |
| Epilimnion-Hypolimnion exchange rate | ($k_{12}$) | 0.02 |
| $H^+$ mass transfer to calcite surface | ($k_D$) | 4.0 |

**Biochemical Forcing Functions**

| | Starting Time (days after January 1) | | | |
|---|---|---|---|---|
| | [b] | 200 | 290 | [c] |
| Net DIC Uptake[d] ($mM\ C \cdot m^{-2} \cdot d^{-1}$) | −2.62 | 0.21 | −2.62 | −1.05 |
| Net Sed. Reduction[e] ($meq \cdot m^{-2} \cdot d^{-1}$) | 0.0 | 0.0 | 0.0 | 1.35 |
| Net Sed. Oxidation[f] ($meq \cdot m^{-2} \cdot d^{-1}$) | 0.23 | 0.23 | 0.23 | 0.0 |
| Sediment Respir.[g] ($mM\ C \cdot m^{-2} \cdot d^{-1}$) | 1.8 | 1.8 | 1.8 | 1.8 |

[a]Value is 0 during ice cover.
[b]Coincides with ice-off.
[c]Coincides with 10 d after ice-on.
[d]DIC uptake (positive value) generates 0.17 meq ANC for every millimole carbon consumption.
[e]Assumes ANC generation (positive value) produces 1.25 mM DIC for every meq ANC produced.
[f]No effect on DIC.
[g]No effect on ANC.

1989), sediment pH in an acid lake typically is not as low as the water column value and does not increase as much as water column pH in response to base addition. Also, carbon dioxide partial pressures within sediments are generally greater than atmospheric, hence, the increased reaction rate due to high carbon dioxide levels is accounted for by making dissolution a function of pore water chemistry.

In addition to dissolving sedimented calcite on the basis of pore water chemistry, inhibition also occurs as a result of sedimentation (burial) of suspended solids settling from the water column (the *SED* term in equation (1)). This process, in effect, transports residual undissolved calcite from the upper, active layer into the lower sediment layer where the impact of calcite dissolution on the water column is minimal.

For the actual dissolution process within the sediments, the generally accepted dissolution reactions for calcite (Plummer et al. 1978) are applied:

$$(2)\quad CaCO_3 + H^+ = Ca^{2+} + HCO_3^-$$

$$(3)\quad CaCO_3 + H_2O + CO_2 = Ca^{2+} + 2HCO_3^-$$

$$(4)\quad CaCO_3 + H_2O = Ca^{2+} + HCO_3^- + OH^-$$

Reaction (2) dominates at pH values less than about 6. Kinetic studies have shown that the reaction rate is transport limited and can be appropriately modeled in this pH range by application of a film mass transport model in which hydrogen ion diffuses through a boundary layer surrounding the particle (Sverdrup and Bjerle 1982). At pH values above 6, reactions (3) and (4) tend to dominate. In addition to the forward reactions, an empirical backward rate expression has been suggested by Plummer et al. (1978) and is included in the overall rate expression for this model. Incorporation of these reaction terms with the transport term yields the following overall dissolution rate expression:

$$(5)\quad d[M]/dt = A_M \{k_D([H^+]\text{-}HSAT) + k_2 [H_2CO_3] + k_3 - k_4 [Ca^{2+}][HCO_3^-]\}$$

where $[M]$ = the mass of undissolved calcite; $k_D$ = the mass transfer coefficient for hydrogen ion penetrating to the calcite surface (metres per day); $k_i$ = reaction rate constants; $A_M$ = the available calcite surface area per unit volume (metres).
It is assumed that all calcite mixed within the sediment layer consists of separate spheres with the available area equal to the sum of all particle surface areas. The reaction rate constants ($k_2$, $k_3$, and $k_4$) are calculated a priori from temperature-dependent empirical formulations given in Plummer et al. (1978). The backward rate expression precludes the possibility of dissolution exceeding saturation (with respect to $CaCO_3(s)$) as well as dampening dissolution rates at high pH and high carbon levels.

A comprehensive review (Plummer et al. 1979) summarizing the available rate constant data indicates a range of values for $k_D$ from 0.26 to 8.28 $m \cdot d^{-1}$. In general these values reflect idealized conditions in well mixed beakers with crystal diameters generally 50 μm or more. An argument can be made to place a low value on this constant, since the hydrodynamic disturbance within sediments is likely to be small (relative to the laboratory studies) and some surface diffusion limitation probably takes place. On the other hand, since $k_D$ is inversely proportional to particle size, the relatively fine calcite (2 μm mean diameter) used in the May 1985 treatments would suggest an increased mass transfer coefficient. These contrasting arguments leave no sound basis for fixing this constant; consequently, a baseline value for $k_D$ of 4 $m \cdot d^{-1}$ (roughly the mean of values quoted by Plummer et al. 1979) was used for the reacidification runs. In any event, because pore water pH levels are generally in the range of 5.5 – 7.0, calcite dissolution becomes increasingly reaction controlled and the transport limited reaction (2) represents a minor percentage of total dissolution contribution.

The reliming of Woods Lake in the fall of 1986, during which a sediment calcite dose of approximately 0.1 $kg \cdot m^{-2}$ was achieved, has led to an increase in treatment duration by at least two-fold. These observations justify the need for considering

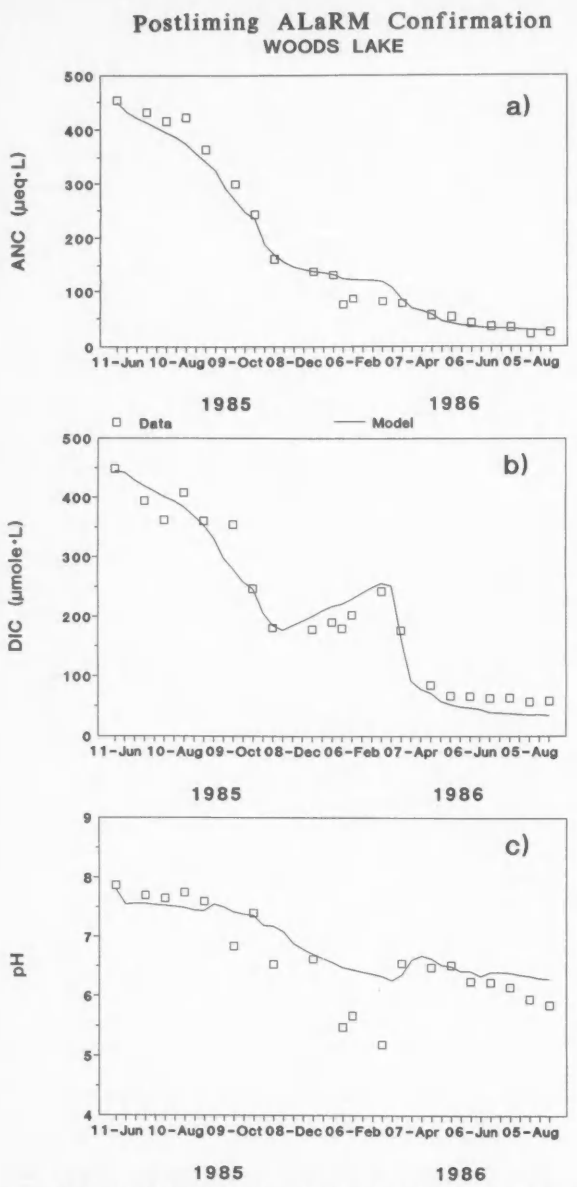


FIG. 5. Results of ALaRM confirmation for Woods Lake water column (a) ANC, (b) DIC, and (c) pH showing comparison of model output and field observations of whole-lake volume-averaged concentrations for the postliming period.

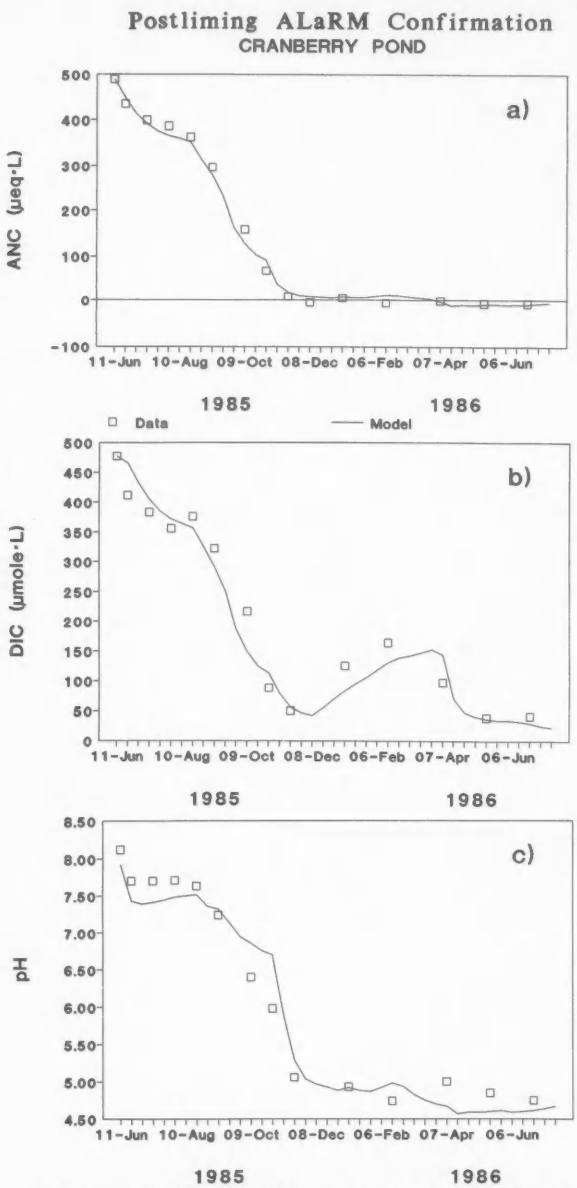


FIG. 6. Results of ALaRM confirmation for Cranberry Pond water column (a) ANC, (b) DIC, and (c) pH showing comparison of model output and field observations of whole-lake volume-averaged concentrations for the postliming period.

sediment neutralization in reacidification predictions, and we are currently field testing this sediment calcite dissolution formulation and its parameterization with these new data.

## Model Confirmation

Confirmation of ALaRM involved comparison of the model predictions with observations for both Woods Lake and Cranberry Pond during the postliming period (June 1985–August 1986). The model predictions for these comparisons (shown in Fig. 5 and 6) were made without changing any coefficients or forcing functions from the calibration values. Only the external loadings and hydrology were adjusted according to *a posteriori* measurement of precipitation quantity and chemistry and its effect on WAM generated loadings; the comparisons thus represent a postaudit confirmation.

In general, the model simulations compare favorably with the field observations of water column volume-averaged ANC, DIC, and pH. This includes the rather rapid decline in ANC and DIC during the fall of 1985 due to the unusually high flush-

TABLE 2. Woods Lake seasonal ANC budget for both pre- and postliming periods.

| Period | ANC load ($eq \cdot d^{-1}$) | Outflow ANC ($eq \cdot d^{-1}$) | Sediment to water flux ($eq \cdot d^{-1}$) | Water column generated ($eq \cdot d^{-1}$) | Water column[c] change ($\mu eq \cdot L^{-1} \cdot d^{-1}$) |
|---|---|---|---|---|---|
| | | | Preliming (Jan. 1984 – May 1985) | | |
| Icecover | −91[a] (29)[b] | 18 (5.7) | 167 (53) | −40.1 (13) | 0.066 |
| Spring melt | −152 (37) | 27 (6.5) | 142 (34) | −92.7 (22) | −0.095 |
| Summer | −9.7 (8.7) | 0.8 (0.75) | 93 (83) | 8.02 (7.2) | 0.081 |
| Fall | −151 (46) | 26 (7.8) | 78 (24) | −71.4 (22) | −0.147 |
| Icecover | −103 (32) | 38 (11) | 143 (44) | −40.1 (12) | 0.047 |
| Spring melt | −294 (49) | 76 (12) | 153 (26) | −74.5 (12) | −0.175 |
| | | | Postliming (June 1985 – Aug. 1986) | | |
| Summer | −42 (4.1) | −733 (72) | −237 (23) | 8.02 (0.8) | −1.250 |
| Fall | −215 (10) | −1680 (80) | −122 (6) | −76 (4) | −2.610 |
| Icecover | −53 (9) | −342 (59) | 135 (23) | −46 (8) | −0.380 |
| Spring melt | −224 (22) | −535 (53) | 154 (15) | −88 (9) | −0.865 |

[a]Negative value indicates a water column sink of positive ANC or a source of negative ANC; positive value indicates a water column source of positive ANC or a sink of negative ANC.

[b]Numbers in parentheses indicate percentage of sum of absolute value of ANC budget terms for a given season.

[c]Water column change may be expressed in units of $eq \cdot d^{-1}$ by multiplying by lake volume ($8.0 \times 10^5\ m^3$) $\times\ 10^{-6}\ eq \cdot \mu eq^{-1}$.

ing and acid input events at this time (Staubitz and Zarriello 1989). As a result Cranberry Pond reacidified to near 0 ANC and pH < 5 by the end of 1985.

Because of its longer hydraulic retention time, Woods Lake still had not completely reacidified (ANC ≅ 25 $\mu eq \cdot L^{-1}$) prior to its reliming in the fall of 1986. In general, ALaRM performed reasonably well in simulating Woods Lake ANC reacidification (Fig. 5a). The major deviation from the ANC field observations occurred during the late winter of 1986, when the model over predicted the whole-lake volume-averaged ANC. This was primarily due to the under prediction by WAM of an acid input event in late January, although over prediction by ALaRM of sediment to water ANC flux during the ice cover period may have contributed to the deviation.

The only other deviation in the Woods Lake confirmation was a slight over prediction of pH during the latter stages of reacidification (Fig. 5c). The higher pH is the result of lower DIC simulations relative to field data at this time. Because the system had a relatively low buffer capacity at this time, a small difference in DIC between model and data, even though ANC concentrations are very close, would lead to a corresponding deviation in pH. Because of elevated primary productivity at this time of the year (Bukaveckas 1989), the upper waters tend to be undersaturated with respect to $CO_2$. This makes it difficult to obtain an accurate measure of *in situ* DIC concentrations and pH because of the strong tendency of $CO_2$ to diffuse into samples before they can be analyzed. It is, therefore, possible that some of this deviation can be attributed to erroneously high DIC data.

## Reacidification Factors

Given that ALaRM produces an accurate simulation of the ANC dynamics of both pre- and postliming periods in Woods Lake, the model can be used to produce a seasonal ANC budget for the lake in order to assess the relative importance of four factors which combine to drive the in-lake ANC changes. Each of these four factors (external acid loading, outflow, sediment-water column exchange, and water column generation/utilization) represents the aggregation of a number of individual processes. Determining which specific processes deserve the most attention in predicting reacidification requires an initial assessment of the relative contribution of the above aggregate factors to the ANC budget of the lake.

Presented in Table 2 is the ALaRM-generated ANC budget for Woods Lake for both the pre- and postliming periods. It presents on a seasonal basis the average daily contribution to the water column ANC change for each of the four factors mentioned above.

In analyzing the ANC budget it is important to note that both the relative and absolute contribution of each factor to the in-lake ANC budget is seasonal and depends on the current in-lake reservoir of ANC (i.e. pre- or postliming). For example, the spring melt period accounts for approximately 40% of the annual acid load to Woods Lake; however, contrary to the preliming period, during the postliming period high spring flows are relatively more significant than the acid load itself in contributing to the water-column ANC change.

During the preliming period, the direction of the change in water column ANC alternated seasonally. Prior to neutralization the ANC budget depended primarily on the balance between the external acid loading to the lake and the sediment-to-water ANC flux. The outflow from the lake is not a major factor, because the ANC concentration in the water column is near 0. Therefore, since approximate steady-state conditions exist for the preliming water column ANC, the net effect of in-lake processes (primarily the positive flux of ANC from the sediments) is the neutralization of much of the external acid input.

As illustrated in Fig. 7a, the net areal flux of ANC from Woods Lake sediments to the water column during the preliming period is positive at all times with peaks coinciding with intense acid loading immediately after ice-off. This is because the largest sediment-water gradient occurs at this time. The

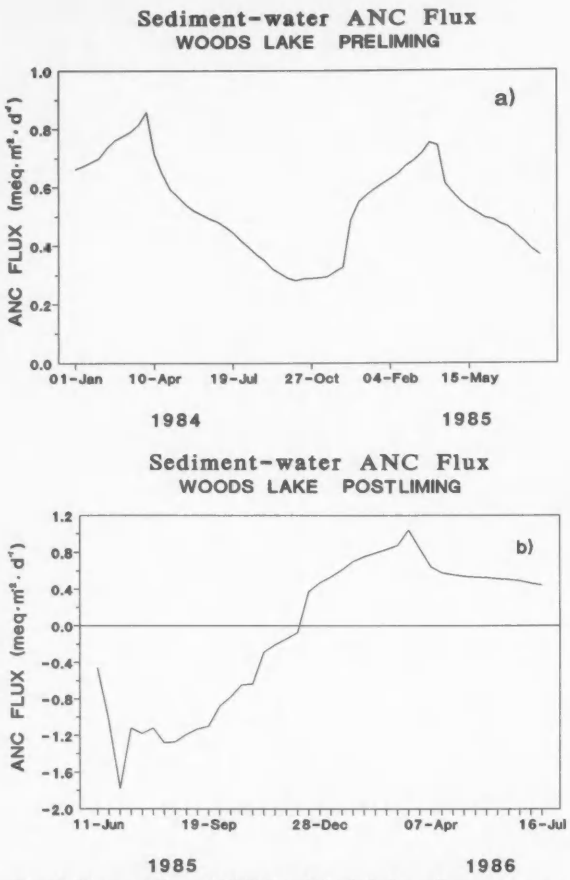


FIG. 7. Net areal flux of ANC from Woods Lake sediments to water column during the (a) preliming period and (b) postliming period. Preliming flux is always positive and compares in magnitude with other acidic lakes; postliming flux is negative (indicating sediment neutralization) for approximately the first 6 mo in response to reversal of the ANC gradient by water column application of calcite.

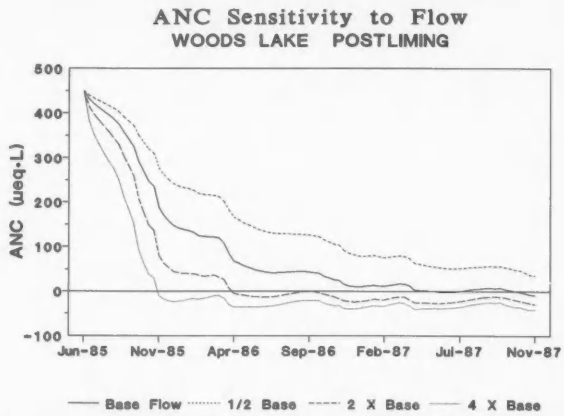


FIG. 8. Sensitivity analysis of Woods Lake reacidification to variation of hydraulic retention time (HRT), generated with ALaRM by adjusting only the flow through the system relative to the actual observed flow for the postliming period. Graph illustrates that a factor of two change in the HRT can make a difference of over a year in reacidification time, but the response is not linear.

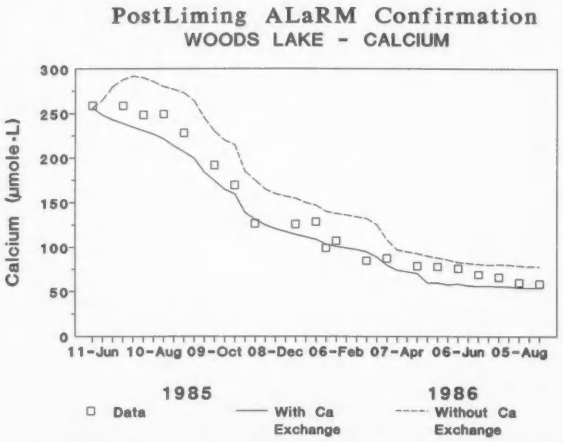


FIG. 9. Comparison of field observations of water column calcium temporal profile (volume-averaged concentrations) with ALaRM simulations with and without a calcium–hydrogen ion exchange process in the sediments. Graph demonstrates that the ion exchange process is primarily responsible for uptake or release of sediment-bound protons in response to pore water fluctuations of acid–base species.

steady flux rise through the winter ice cover period corresponds to the sediment ANC build-up due to various reduction processes that occur as sediment anaerobic conditions develop under the ice cover. The mean yearly values of sediment-to-water ANC fluxes (194 and 240 meq·m$^{-2}$·yr$^{-1}$ for Woods Lake and Cranberry Pond, respectively) compare favorably with those reported by Schiff and Anderson (1986) for the epilimnetic sediments of nine Experimental Lakes Area (northwestern Ontario) study lakes (values ranged from $-15$ to 510 (mean of 137) meq·m$^{-2}$·yr$^{-1}$). The fluxes are virtually identical to the value of 207 meq·m$^{-2}$·yr$^{-1}$ calculated by Carignan (1985) from sediment core profiles in Clearwater Lake (near Sudbury, Ontario).

During the postliming reacidification period, the net change in water column ANC was always negative. Its magnitude was controlled largely by hydrologic outflow. The very large loss of ANC through the outlet of the lake in the fall of 1985 was due to a combination of high ANC concentrations still in the water column at that time and the unusually high fall flows (Staubitz and Zarriello 1989; Driscoll et al. 1989). Figure 8 demonstrates that Woods Lake reacidification is very sensitive to its hydrology; a factor of two change in the flow through the system can make a difference of at least a year in the reacidification time.

It is also worth noting that during the postliming period the sediment to water ANC flux reversed in mid-December from a rather large negative flux shortly after the liming to a positive flux similar in magnitude to the preliming flux (Fig. 7b). Obviously, this was the result of a reversal in the water column–sediment pore water ANC gradient, induced partially by the rapid ANC decrease in the water column through the fall and partially by the increase in pore water ANC as a result of sediment neutralization (Young et al. 1989). It is our belief that the sediment neutralization occurred by a combination of dissolu-

tion of the small amount of undissolved calcite that entered the sediments during the 1985 treatment and the mass transfer of alkalinity species (accompanied by an equivalent amount of calcium) from the water to the sediments occurring during the first 6 mo after treatment.

The large buffer capacity of the sediment pore water relative to the overlying water column (resistance to pH change during influx of alkalinity) can be explained by a release of sediment-bound protons (via ion exchange with calcium among other possible processes) that neutralize the increased alkalinity species. Evidence of this process is given in Fig. 9. If we do not assume that calcium exchanges with the sediment-bound protons, then there is a buildup of pore water calcium which, by virtue of decreasing the water-sediment gradient, inhibits the transfer of calcium from the water column to the sediments. As a result, ALaRM over predicts the water column levels during the early part of the postliming period. If, on the other hand, for every sediment-bound proton that is released to the pore water an equivalent amount of calcium is immobilized to balance charge, then a satisfactory water column simulation is obtained.

The difference between the slopes of the two calcium simulations at any point in time represents the significance of this process as a function of time through the reacidification. The relatively large deviation early in the reacidification period is consistent with the large transfer of ANC to the sediments during the 3 summer mo after treatment (see Table 2). Later in the reacidification period, as the sediments themselves began to reacidify (Young et al. 1989), some of the calcium and associated ANC that earlier had been transferred into the sediments was released back into the water column. In this particular case then, the net effect of sediment-water materials fluxes on the reacidification rate of Woods Lake was not very significant.

## Conclusions

Reacidification modeling for calcite treated acid lakes is an integral part of: (1) assessment of the feasibility of whole-lake liming as a mitigative strategy for lake acidification; (2) optimization of treatment strategy and planning of reapplication for individual lake systems; and (3) development of a regional water resource management program that includes base addition as a restoration and/or preventive measure. In using ALaRM to evaluate the relative contributions of several factors to the reacidification of Adirondack drainage lakes (such as Woods Lake), it was determined that flushing of ANC from the lake, as governed by watershed morphologic and hydrologic characteristics, was the primary factor. The next factor in order of significance was sediment-water ANC transfer. This flux represented a relatively large sink of water column ANC during the first 6 mo of reacidification, followed by a reversal to the more often observed ANC source for the duration of the post-treatment period. These findings suggest that the greatest improvements in reacidification modeling of limed lakes would come from a better understanding and/or parameterization of those processes that control the hydrology of a watershed and, secondarily, those processes that affect *in situ* water column and sediment acid–base chemistry.

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# Production and Growth Efficiency of Brook Trout (*Salvelinus fontinalis*) in Two Adirondack Mountain (New York) Lakes Following Liming[1]

Carl L. Schofield, Steven P. Gloss, Barbara Plonski, and Robert Spateholts

*Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, NY 14853, USA*

Schofield, C. L., S. P. Gloss, B. Plonski, and R. Spateholts. 1989. Production and growth efficiency of brook trout (*Salvelinus fontinalis*) in two Adirondack mountain (New York) lakes following liming. Can. J. Fish. Aquat. Sci. 46: 333–341.

Yearling and spring fingerling brook trout (*Salvelinus fontinalis*) stocked in two Adirondack lakes after liming in the spring of 1985 produced 10–14 $kg \cdot ha^{-1} yr^{-1}$ at average standing crops of 8–10 $kg \cdot ha^{-1}$ during the first year after stocking. These values were similar to levels observed in other limed and circumneutral Adirondack lakes, which collectively support a limited range of biomass (10–20 $kg \cdot ha^{-1}$) and production (7–16 $kg \cdot ha^{-1}$) compared with more fertile waters in other regions. The estimated level of food consumption required to maintain initial production rates observed in the two limed lakes was 80–100 $kg \cdot ha^{-1}$. This level of predation was sufficient to significantly alter the size structure and composition of the invertebrate prey community within a few months after stocking. However, mean production efficiency in these populations remained at levels of 20–25% and the development of adverse water quality conditions in the first year after liming appeared to be of greater significance than food limitation in regulating production and biomass of these stocked brook trout populations. Reacidification of one lake 5 mo after liming resulted in rapid declines in biomass and production as a result of both increased mortality and reduced growth.

Des ombles de fontaine de classe d'âge 1+ et du stade truitelle de printemps lâchés dans deux lacs des Adirondacks traités au moyen d'un agent neutralisant au printemps de 1985 ont produit une biomasse de 10–14 $kg \cdot ha^{-1} \cdot an^{-1}$ avec une moyenne de 8–10 $kg \cdot ha^{-1}$ l'année suivant l'ensemencement. Ces valeurs sont semblables à ce qu'on a mesuré dans d'autres lacs des Adirondacks dont les eaux ont été traitées et sont proches du point de neutralité; dans l'ensemble, la plage des valeurs de biomasse (10–20 $kg \cdot ha^{-1}$) et de production (7–16 $kg \cdot ha^{-1} \cdot an^{-1}$) est assez limitée dans ces lacs par comparaison à des eaux plus riches, dans d'autres régions. On estime à 80–100 $kg \cdot ha^{-1} \cdot an^{-1}$ la consommation de nourriture nécessaire au maintien du taux de production initial mesuré dans les deux lacs traités. À ce rythme, la prédation était suffisamment intensive pour que la répartition et la composition de la communauté d'invertébrés visée par les prédateurs se modifient dans une mesure significative quelques mois après l'ensemencement. Néanmoins, la production moyenne de ces populations est restée à 20–25 % et l'altération de la qualité de l'eau qui s'est produite durant l'année suivant le traitement semble avoir eu plus d'influence que la réduction des ressources alimentaires dans la régulation de la production et de la biomasse des populations d'ombles ensemencés. L'un des deux lacs étudiés était réacidifié cinq mois après le traitement : il s'en est suivi une baisse rapide de la biomasse et de la production à cause de l'augmentation de la mortalité et du ralentissement de la croissance.

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Several whole lake liming experiments have adequately demonstrated enhanced survival of fish populations (stocked and indigenous) in acidified lakes following neutralization (Hasselrot et al. 1984; Molot et al. 1984; Schofield et al. 1986; Gloss et al. 1989). However, the suitability of liming as a management tool for reestablishment of fish populations in acidified waters is also dependent on maintenance of adequate levels of recruitment and growth. Recruitment can be effectively controlled in brook trout (*Salvelinus fontinalis*) populations through adjustment of stocking rates and/or regulation of natural reproduction (Webster and Flick 1981). Fish growth is a more volatile parameter that is less amenable to direct manipulation. A wide range in growth responses in limed Adirondack lakes (both temporal and between lakes) has been reported (Schofield et al. 1986), which reflects both physiological effects of varying water quality after liming and levels of food availability.

Production provides an integrated measure of the effects of these environmental variables on both survival and growth at the population level, and is amenable to analysis of those factors most important in the regulation of biomass. In this paper we provide a description of the levels of brook trout production and biomass observed in Woods Lake and Cranberry Pond over the first 16 mo following liming and stocking. These two Adirondack lakes selected for study were included in the Lake Acidification Mitigation Project (LAMP) described by Porcella (1989). The production process during this period was analyzed

[1]This is part of a series of 13 papers devoted to the Lake Acidification Mitigation Project.

TABLE 1. Constants and values for coefficients used in the growth model (data from Kerr 1971a,b except * derived from pooled sample of 246 trout from Woods Lake and Cranberry Pond.

| Parameter | Value | Description |
|---|---|---|
| $a$* | 0.046 | Coefficient of length (m) – weight (g) relationship. |
| $b$* | 0.336 | Exponent of length (m) – weight (g) relationship. |
| $m$ | 0.2882 | Fraction of ration used for calorigenic metabolism. |
| $s$ | 9.072E-12 | Coefficient relating swimming speed to energetic cost. |
| ρ | 0.8 | Assimilation efficiency. |
| $k$ | 86400 | Coefficient relating swimming speed to fish length. |
| $\alpha_s$ | 0.0012*$T$(°C) | Standard metabolism coefficient. |
| λ | 0.85 | Weight exponent of metabolism. |

TABLE 2. Range of prey energy contents used in model calculations of prey selection and trout ration.

| Taxa | Energy content (cal) |
|---|---|
| Anisoptera | 10–40 |
| Zygoptera | 4–10 |
| Trichoptera | 3–8 |
| Coleoptera | 2–6 |
| Megaloptera | 5–17 |
| Hemiptera | 2–8 |
| Diptera | 0.5–3.5 |
| Ephemeroptera | 1–4 |
| Acarina | 1–5 |
| Amphipoda | 0.1–0.5 |
| Cladocera | 0.01–0.03 |

in more specific terms with the aid of an analytical growth model (Kerr 1971a), which provided a means of estimating food intake and the aid of optimal foraging theory as presented by Werner and Hall (1974). The specific objective of this analysis was to assess the effects of changes in prey community structure on production efficiency of the stocked trout populations.

## Methods

### Biomass and Production

Biomasses of the 1984 and 1985 year-classes of brook trout stocked in Woods Lake and Cranberry Pond were determined as the product of estimated population sizes and mean weights of the cohorts sampled by trapnet during the semiannual inventory periods in 1985 and 1986 (Gloss et al. 1989). Variance and 95% confidence intervals for biomass estimates were obtained as described by Chapman (1967). For comparisons between lakes areal units ($kg \cdot ha^{-1}$) of biomass, production, and rations were calculated using lake surface areas given by Staubitz and Zarrielo (1989).

Production is defined as the total elaboration of tissue by the population per unit time (Chapman 1967) and was estimated as the product of instantaneous growth ($G$) and mean biomass ($\bar{B}$) between semiannual inventory periods. Instantaneous rates of growth, mean biomass, and appropriate variance estimators were calculated as described by Ricker (1975).

### Estimation of Food Consumption and Prey Selection

The balanced energy equation of Winberg (1956) was utilized as the basis for estimation of ration intake by individual fish in the population on a daily basis,

$$(1) \quad \rho R = T_T + \Delta W$$

where the energy of growth ($\Delta W$) and total metabolism ($T_T$) are equated to the energy assimilated (ρ being assimilation efficiency) from the ingested ration ($R$). Daily growth was estimated from the instantaneous growth coefficients and mean weights of the cohorts at the beginning of each period. Transformations to energy equivalents were based on the assumptions that 1 g wet weight of fish tissue yields 1 kcal and assimilation efficiency is 0.8 (Mann 1965). The energy expended in metabolism can be described as a function of body weight ($W$),

$$(2) \quad T_T = \alpha_t W^{\lambda}$$

where the average value of the exponent λ is relatively stable at values of 0.8–0.9 for most fish species (Paloheimo and Dickie 1966). We utilized a value of 0.85 for λ, suggested by Kerr (1971a) as an appropriate value for brook trout. The coefficient $\alpha_t$ represents the metabolic level and it is sensitive to temperature, level of activity, and ration intake (Beamish 1964). Substitution of equation 2 for $T_T$ in equation 1 and a representation for $R$ provided by Kerr (1971b), which is a function of metabolic level, yields an equation that was solved by an iterative procedure for $\alpha_t$,

$$(3) \quad \rho(W_p(\alpha_t - \alpha_s)W^{\lambda}/(sQWLk + mW_p)) - \alpha_t W^{\lambda} - \Delta W = 0$$

where $W_p$ is the mean energy content of prey (kilocalories), $L$ is fish length (metres), $Q$ is the mean distance travelled between prey items constituting the daily ration (a function of prey size and density), and the remaining terms and coefficients are as described in Table 1 and as described by Kerr (1971a,b). The primary variables that determine metabolic level (and hence $R$) in this function are fish growth and size, temperature, prey energy content, and prey density. Kerr (1971c) simulated growth of lake trout for given prey energy contents and densities by assigning levels of $\alpha_t$ in his model using an iterative routine that maximized the ratio of $K/R$, where $K$ is the estimated growth efficiency ($\Delta W/R$). The rationale for this procedure was that size selective predators exhibit a tendency to maximize growth efficiency, but at the same time intraspecific competition tends to reduce ration intake to a minimum. We accepted this rationale as the basis for prey selection from the array of invertebrates known to compose the diet of the brook trout populations in our study lakes (Gloss et al. 1989). This protocol is consistent with optimal foraging theory as discussed by Werner and Hall (1974) and differs from Kerr's (1971c) algorithm in that no assumption concerning the relationship of metabolic level to the $K/R$ ratio is required. Ration and growth efficiency were computed directly from equation 3 for each potential prey species, utilizing approximations of initial densities and mean energy content (Table 2) at the beginning and end of each period (Evans 1989). A simple model of exponential growth without recruitment and the assumption that all prey mortality was due to fish predation was utilized to simulate changes in prey stocks within periods. In this model, fish selected the prey species, on a daily basis, that yielded the maximum ratio of $K/R$. The estimated ration was computed for the population based on the number of fish present on each day and then deducted from the biomass of the selected prey species. Cumulative rations were tallied by

TABLE 3. Estimated number($N$), mean individual weight($w$), and biomass ($B$) of 1984 year-class Temiscamie and 1985 year-class Domestic × Temiscamie brook trout in Woods Lake and Cranberry Pond during 1985–86. (Numbers in parenthesis are standard errors of mean $w$ and 95% confidence intervals for $N$ and $B$.)

| | | Woods Lake | | | Cranberry Pond | | |
|---|---|---|---|---|---|---|---|
| Period | Year class | $N$ | $w$(g) | $B$(kg·ha$^{-1}$) | $N$ | $w$(g) | $B$(kg·ha$^{-1}$) |
| 6/3/85–6/4/85 | 1984 | 1200[a] | 160 | 8.3 | 400 | 160 | 8.9 |
| | | | (2.2) | (0.2) | | (2.2) | (0.3) |
| | 1985 | 5000[a] | 3.2 | 0.7 | 2000 | 3.2 | 0.9 |
| | | | (0.8) | (0.1) | | (0.8) | (0.1) |
| 9/30/85–10/31/85 | 1984 | 543 | 176 | 4.2 | 217 | 237 | 7.2 |
| | | (408–817) | (2.6) | (1.8) | (146–436) | (4.7) | (3.6) |
| | 1985 | 2034 | 32 | 2.8 | 1236 | 51 | 8.7 |
| | | (1434–3003) | (0.8) | (2.3) | (889–1781) | (0.9) | (6.6) |
| 4/15/86–5/1/86 | 1984 | 256 | 236 | 2.6 | | | |
| | | (189–359) | (4.0) | (1.8) | | | |
| | 1985 | 1725 | 96 | 7.2 | 164 | 65 | 1.5 |
| | | (1216–2547) | (1.8) | (6.0) | (68–394) | (1.8) | (4.2) |
| 9/22/86–10/16/86 | 1984 | 10 | 312 | 0.14 | | | |
| | | (3–100) | (20.4) | (0.4) | | | |
| | 1985 | 385 | 193 | 3.2 | 9[b] | 213 | 0.3 |
| | | (280–619) | (2.4) | (1.2) | | (24.2) | (0.4) |

[a]Number stocked in each lake.
[b]Total number caught 9/22/86–10/2/86

TABLE 4. Mean biomass ($\bar{B}$), instantaneous growth rate ($G$), and production ($P$) of 1984 year-class Temiscamie and 1985 year-class Domestic × Temiscamie brook trout in Woods Lake and Cranberry Pond during 1985–86. (Numbers in parenthesis are variance of $G$ and 95% confidence intervals for $B$ and $P$).

| | | Woods Lake | | | Cranberry Pond | | |
|---|---|---|---|---|---|---|---|
| Period | Year class | $G$ | $B$(kg·ha$^{-1}$) | $P$(kg·ha$^{-1}$·yr$^{-1}$) | $G$ | $B$(kg·ha$^{-1}$) | $P$(kg·ha$^{-1}$·yr$^{-1}$) |
| 6/85–10/85 | 1984 | 0.0952 | 6.0 | 0.6 | 0.3927 | 8.0 | 3.1 |
| | | (0.0004) | (0.9) | (0.3) | (0.0006) | (1.8) | (0.8) |
| | 1985 | 2.3026 | 1.5 | 3.5 | 2.7687 | 3.4 | 9.5 |
| | | (0.0007) | (1.2) | (2.1) | (0.0001) | (2.3) | (6.1) |
| 10/85–5/86 | 1984 | 0.2934 | 3.3 | 1.0 | | 4.0 | |
| | | (0.0005) | (1.3) | (0.4) | | (0.9) | |
| | 1985 | 1.1038 | 4.7 | 5.1 | 0.2426 | 4.1 | 1.0 |
| | | (0.0010) | (2.9) | (3.0) | (0.0010) | (1.8) | (0.8) |
| 5/86–10/86 | 1984 | 0.2792 | 0.8 | 0.2 | | | |
| | | (0.0046) | (0.5) | (0.1) | | | |
| | 1985 | 0.6931 | 5.0 | 3.5 | 1.1869 | 0.7 | 0.8 |
| | | (0.0005) | (2.5) | (2.1) | (0.0136) | (2.0) | (2.2) |

TABLE 5. Comparisons of instantaneous daily growth rates ($G$) for 1984 and 1985 year-classes in Woods Lake and Cranberry Pond. (Variances $V(G)$ compared with $Z$ statistic).

| | | 1985 Year Class | | 1984 Year Class | |
|---|---|---|---|---|---|
| Period | | Woods Lake | Cranberry Pond | Woods Lake | Cranberry Pond |
| 6/85–10/85 | $G$ | 0.0193 | 0.0232 | 0.0008 | 0.0033 |
| | $V(G)$ | 6.1e–6 | 1.1e–6 | 3.5e–6 | 4.9e–6 |
| | $Z$ | 1.45 | | 8.65[a] | |
| 10/85–5/86 | $G$ | 0.0054 | 0.0012 | 0.0014 | |
| | $V(G)$ | 2.7e–6 | 5.0e–6 | 2.5e–6 | |
| | $Z$ | 1.51 | | | |
| 5/86–10/88 | $G$ | 0.0043 | 0.0074 | 0.0017 | |
| | $V(G)$ | 3.0e–6 | 8.5e–5 | 2.8e–5 | |
| | $Z$ | 0.33 | | | |

[a]$P < 0.001$.

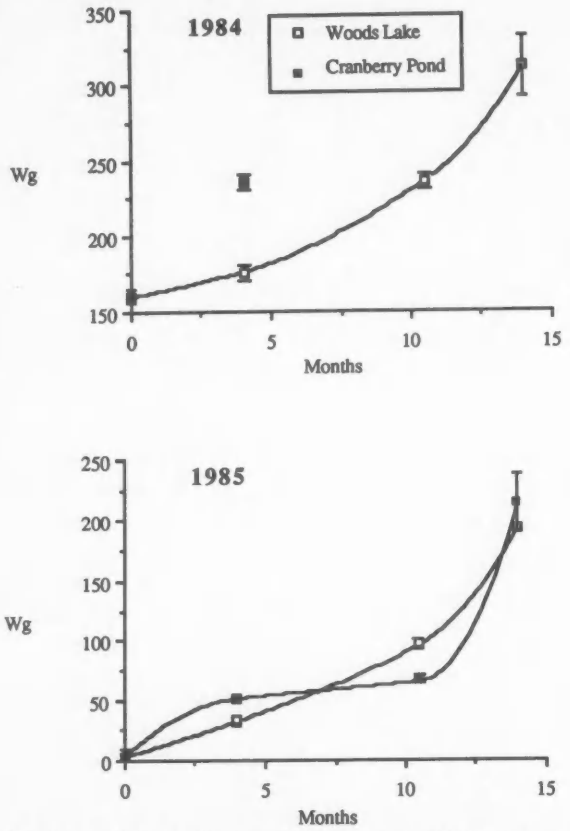


FIG. 1. Growth in weight (mean and standard error) of 1984 year-class Temiscamie brook trout and 1985 year-class Domestic × Temiscamie brook trout in Woods Lake and Cranberry Pond from stocking 6/85 to 10/86.

prey taxa to estimate total food consumption by cohorts and the relative contributions of prey taxa to fish production over each period.

## Results and Discussion

### Biomass and Production

The total biomass of yearling and spring fingerling brook trout stocked in Woods Lake and Cranberry Pond, following liming in the spring of 1985, was approximately equal in both ponds at 9–10 kg·ha$^{-1}$ (Table 3). The yearling Temiscamie cohort constituted more than 90% of this initial biomass in both ponds. Subsequent changes in biomass were mediated by differential seasonal patterns of growth and survival of these cohorts in the two lakes.

During the first summer following liming, the trout population in Woods Lake experienced a 22% net loss in biomass, whereas a net gain in biomass of 62% was observed in Cranberry Pond (Table 3). Production during this period was approximately three times greater in Cranberry Pond than in Woods Lake (Table 4). Growth rates of the 1985 year class were not significantly different ($P<0.05$) in the two lakes during this period (Table 5). However, higher survival in Cranberry Pond (62%) than in Woods Lake (41%) was primarily responsible for

TABLE 6. Model estimates of total ration ($R$ kcal·10$^{-3}$·ha$^{-1}$), food consumption rate ($Rd$ cal·kcal$^{-1}$·d$^{-1}$), and gross growth efficiency ($P/R$) for 1984 year-class Temiscamie and 1985 year-class Domestic × Temiscamie brook trout in Woods Lake and Cranberry Pond during 1985–86. Rations estimated for fixed temperatures of 15°C during summer periods and 5°C during winter.

| | | Woods Lake | | | Cranberry Pond | | |
|---|---|---|---|---|---|---|---|
| Period | Year class | *R* | *Rd* | *P/R* | *R* | *Rd* | *P/R* |
| 6/85–10/85 | 1984 | 10.8 | 15 | 0.05 | 18.8 | 20 | 0.17 |
| | 1985 | 10.4 | 58 | 0.34 | 26.2 | 65 | 0.36 |
| 10/85–5/86 | 1984 | 4.9 | 7 | 0.20 | | | |
| | 1985 | 15.2 | 16 | 0.34 | 6.4 | 8 | 0.16 |
| 5/86–10/86 | 1984 | 2.2 | 18 | 0.11 | | | |
| | 1985 | 18.0 | 22 | 0.19 | 3.3 | 30 | 0.25 |

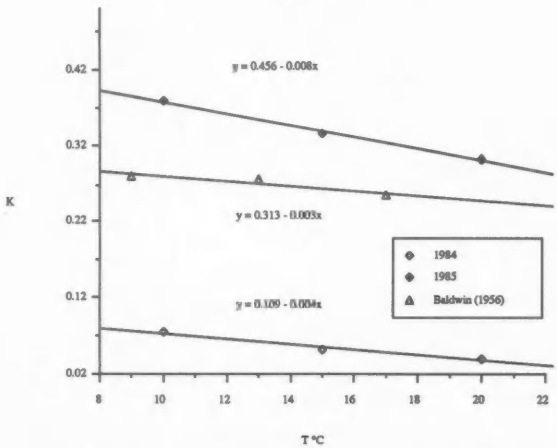


FIG. 2. Effects of mean water temperature on model estimates of growth efficiency ($K = \Delta W$/Ration) for the 1984 and 1985 year-classes of brook trout in Woods Lake during the period 6/85–10/85 and experimental data for yearling domestic brook trout from Baldwin (1956).

increased production rates of this cohort. Growth of the 1984 year class was significantly less in Woods Lake than in Cranberry Pond (Table 5) resulting in a five-fold greater production rate by this year-class in Cranberry Pond. Production by the 1985 year-class accounted for 75 and 85% of the total production in Cranberry Pond and Woods Lake over this 4-mo period.

Following the reacidification of Cranberry Pond in the fall of 1985 (Driscoll et al. 1989), drastic reductions in biomass and production were observed as a result of both increased mortality rates (Gloss et al. 1989) and reduced growth. No trout from the 1984 year-class were captured in Cranberry Pond after the fall 1985 inventory, which preceded the reacidification, and survival of the 1985 year-class was very low (13%). Growth of the surviving fish in the 1985 year-class declined significantly during winter (Fig. 1, Table 5) and production decreased 10-fold (Table 4). Although growth rate of the 1985 year-class also decreased in Woods Lake during winter (Table 5), improved growth of the 1984 year-class and increased survival of both cohorts resulted in increased levels of total biomass and production (Table 4).

Growth rates of trout in Woods Lake did not change significantly during the summer of 1986 compared with the

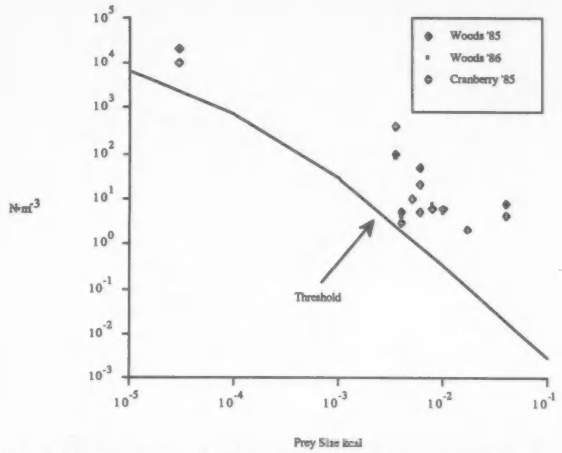


FIG. 3. Densities of prey for the range of prey sizes consumed by brook trout in Woods Lake and Cranberry Pond, below which significant variations in model estimates of ration and growth efficiency occur. Line represents model theshold and points are initial densities input to model.

previous winter (Table 5) and further declines in biomass and production during this period (Table 4) were accentuated by low survival rates (Gloss et al. 1989). The few surviving trout of the 1985 year-class captured in Cranberry Pond in the fall of 1986 were in excellent condition and exhibited a marked improvement in growth (Fig. 1), despite continued levels of high acidity during this period (Driscoll et al. 1989).

## Food Consumption and Prey Selection

Estimates of the amount and composition of prey consumed by trout in Woods Lake and Cranberry Pond were obtained for summer and winter periods corresponding to those used for production calculations (Table 6). The primary variables in the growth model that determined metabolic levels and resulting estimates of rations and growth efficiency were temperature, prey size, and prey density. The relative importance of the assigned values of these variables to the estimates of ration and growth efficiency for trout in Woods Lake and Cranberry Pond are discussed below. The levels of metabolism (expressed as a multiple of standard metabolism) that were generated by the model ranged from 1.6–2.1 for 1984 year-class brook trout and 1.8–2.8 for the 1985 cohort. These levels agree with empirical observations of metabolic levels for other fishes (Winberg 1956; Mann 1969) and are similar to the range obtained by Kerr (1971c) for simulated growth of lake trout.

## Temperature Effects

Metabolism, activity, and food consumption rates are all significantly affected by water temperature. Graham (1949) reported preferred temperatures for brook trout to be 14–19°C and Baldwin (1956) observed maximum growth and food consumption rates at 13°C, for brook trout fed live minnows in a laboratory environment. More recently, Cone (1987) utilized vertical gill nets to evaluate the summer distribution of brook trout in a small, thermally stratified Adirondack pond. He observed a strong preference by Temiscamie and Assinica strain brook trout for metalimnetic zones with temperatures of 10–15°C. Summer temperatures of oxygenated waters in Woods

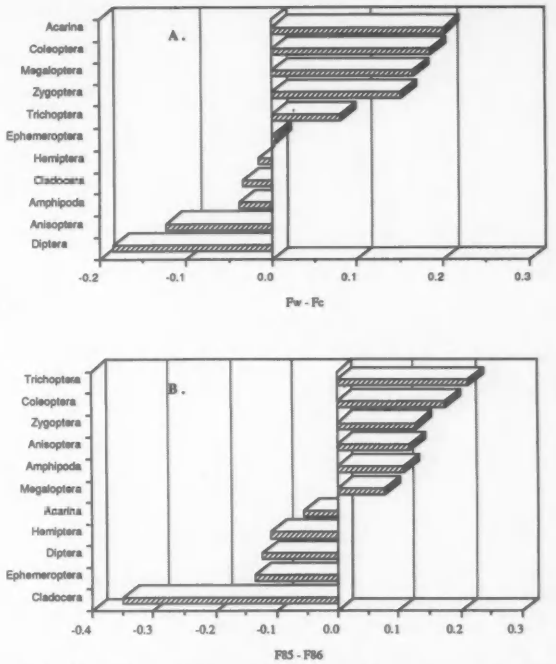


FIG. 4. Comparison of observed frequency of occurrence of major prey taxa in the diets of trout in Woods Lake and Cranberry Pond during the (A) summer of 1985 and comparison of frequency of occurrence of prey taxa in the diet of Woods Lake trout during the (B) summers of 1985 and 1986. Values plotted are differences in frequency of occurrence.

Lake and Cranberry Pond ranged from 10–22°C and early spring water temperatures were 0–8°C (Fordham and Driscoll 1989). The model estimates of rations and growth efficiency presented in Table 6 were based on fixed temperatures of 15°C for the summer periods of 1985–86 and 5°C for the fall, 1985 to spring, 1986 period. The effects of temperature, in the range of 10–20°C, on estimated growth efficiencies for the 1984 and 1985 cohorts in Woods Lake (Fig. 2) illustrate the magnitude of the variance (4–8%) in estimated growth efficiency associated with the unknown distribution of brook trout across this temperature gradient. Baldwin (1956) found a similar inverse relationship between temperature and growth efficiency for yearling brook trout, that he attributed to increasing metabolic costs for maintenance at higher temperatures (Fig. 2).

## Effects of Prey Energy Content and Density

The prey organisms consumed by brook trout in Woods Lake and Cranberry Pond were assigned initial densities based on approximations of relative abundance of these organisms in the nekton and benthos (Evans 1989). These assigned prey densities were well above the threshold levels in the model, below which estimated rations and growth efficiency would be significantly affected by variations in density (Fig. 3). Kerr (1971c) also noted the relative insensitivity of the model to prey density and suggested that trout growth could be essentially independent of prey density, if relatively low threshold levels of abundance were met. Prey size appeared to be a more important determinant of growth efficiency and maximum attainable size for salmonids (Kerr 1971b). However, given the small size

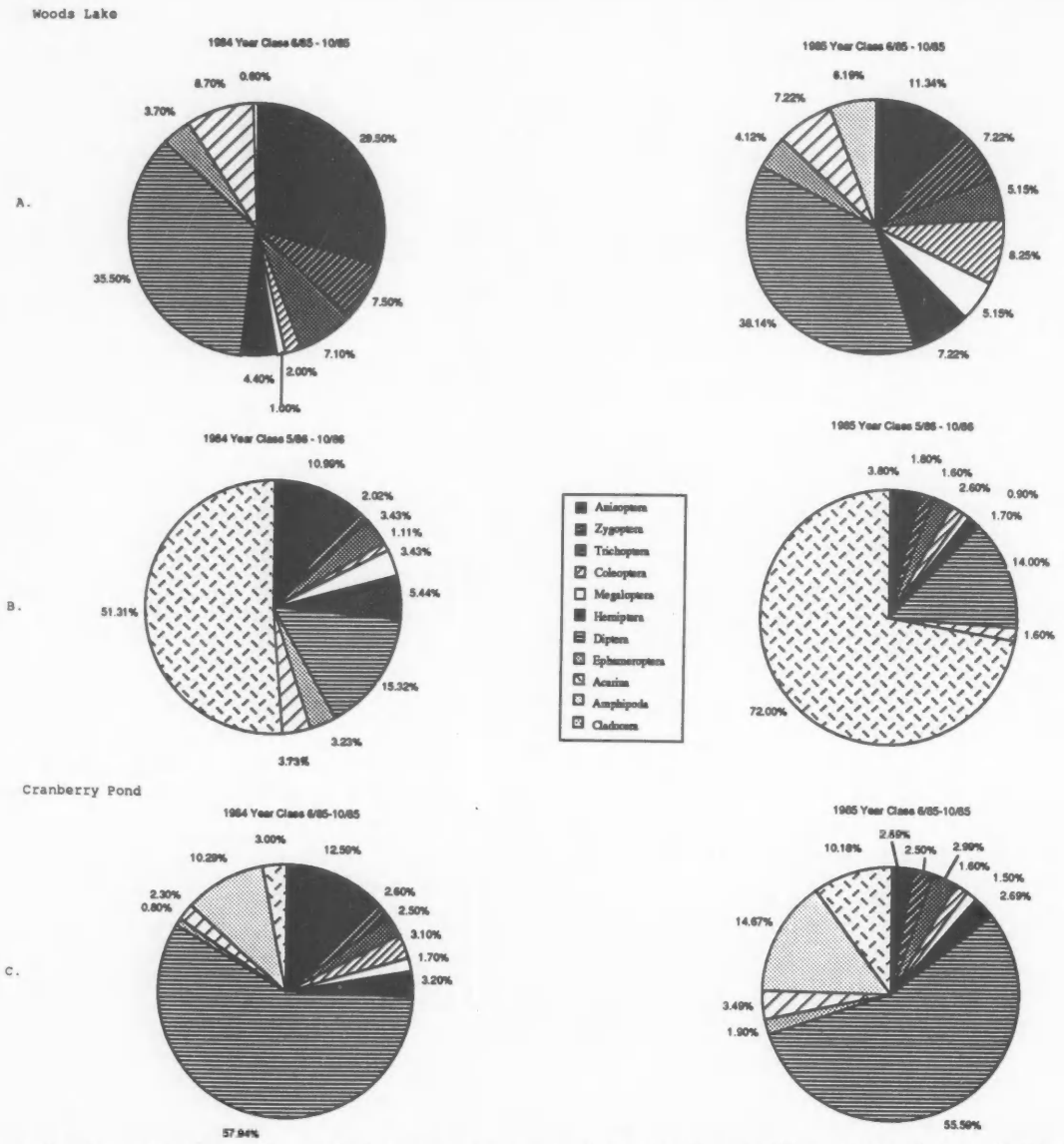


FIG. 5. Growth model estimates of the contributions of prey taxa to production by the 1984 and 1985 year-classes of trout in (a) Woods Lake during the period 6/85–10/85, (b) Woods Lake during the period 5/86–10/86 and (c) Cranberry Pond during the period 6/85–10/85.

of trout that were age II and younger in the two study lakes, relative to the range of sizes available in the invertebrate prey community, variations in prey energy content had little effect on estimated ration levels. For example, either a diet composed entirely of zooplankton (1 *e*–5 kcal) or odonates (1 *e*–2 kcal), at constant densities above the thresholds shown in Fig. 3 would have resulted in estimated total ration levels within $\pm 2$ kg·ha$^{-1}$ of the estimates given in Table 6 for the fish in Woods Lake.

## Prey Selection Patterns

Differences in the diets of trout in Woods Lake and Cranberry Pond during 1985 and in Woods Lake between 1985 and 1986 were described by Gloss et al. 1989. Frequency of occurrence data (Fig. 4) illustrate the relative importance of major prey taxa in the diets of Cranberry Pond and Woods Lake brook trout and also the shift in diet composition in Woods during 1986. The primary difference between diets of trout in Woods Lake and Cranberry Pond is the relatively greater importance of dipterans (specifically *Chaoborus*) in Cranberry Pond. In Woods Lake, the shift in diet during 1986 from larger macroinvertebrates to smaller prey, such as Cladocera, is of particular interest. The model runs employed to estimate rations for trout in the two lakes also yielded estimates of the relative contributions of major prey items to production by the 1984 and 1985 cohorts (Fig. 5). In general, these simulations reflected the

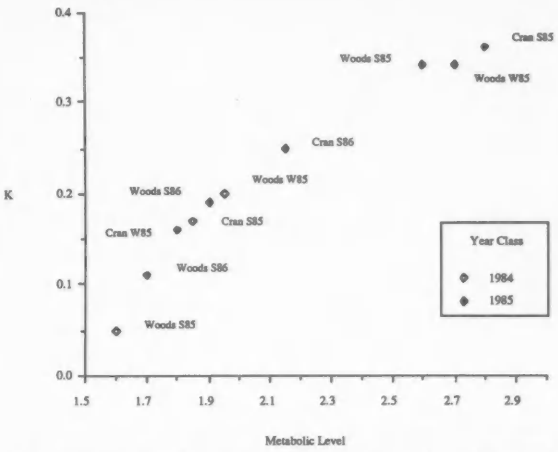


FIG. 6. Average growth efficiency ($K$) as a function of metabolic level (multiple of standard metabolism) for 1984 and 1985 year-classes of brook trout in Woods Lake and Cranberry Pond for (W) winter and (S) summer periods during 1985–86.

observed prey utilization patterns described above. More than 50% of the trout production in Cranberry Pond during 1985 was derived from consumption of dipterans, as compared with approximately 35% in Woods Lake (Fig. 5a, c). The observed shift from larger macroinvertebrates to smaller prey in Woods Lake during 1986 was also simulated by the model (Fig. 5b). The cladoceran contribution to trout production in 1985 was less than 1% and increased dramatically in 1986 to 51–72%. The comparatively small differences in prey utilization patterns between cohorts generated by the model were not detected in the observed diet analysis (Gloss et al. 1989). Although prey size and density did not markedly affect the estimated total rations, the simulated contributions of the various prey taxa to total production were strongly influenced by the array of prey sizes and relative initial densities used in the model. The general agreement between observed and simulated patterns of prey selection at least qualitatively supports the model algorithm of optimal foraging based on selection of prey that yield the highest growth efficiency for the minimum ration intake.

### Growth Efficiency

The estimated ration levels, food consumption rates, and growth efficiencies varied markedly between lakes, cohorts, and seasons (Table 6). The relationship of growth efficiency to metabolic levels (multiple of standard metabolism) estimated by the model is shown in Fig. 6. Similar maximum levels of metabolism, food consumption rates, and growth efficiency were exhibited by the 1985 year-class trout during the first summer after stocking in both Woods Lake and Cranberry Pond. During this same period, metabolic levels, food consumption rates, and growth efficiency were considerably lower for the larger Temiscamie strain trout of the 1984 year-class. However, in contrast with the comparable response of the 1985 year-class in both lakes, very low growth efficiency and a level of metabolism just above maintenance requirements were estimated for the 1984 year-class in Woods Lake relative to that in Cranberry Pond.

Improved growth efficiency occurred in this cohort during winter and to a lesser extent during the summer of 1986. In view of the apparently adequate food resources present initially in Woods Lake, this anomalous situation suggests that environmental factors such as the pronounced water quality and temperature gradients that persisted in Woods Lake during the first summer after liming (Fordham and Driscoll 1989), may have affected the distribution of this cohort relative to its food supply and optimal water quality zone. Fish captured during short-term gillnet sets for diet analyses during September and October 1985 were larger than fish from the same 1984 year-class captured over a longer period by trapnet during the same months (mean weight in gill nets $198 \pm 14$ g versus $176 \pm 5$ in trapnets). Because gear selectivity for fish size was not apparently a factor in this situation (no significant difference in mean weights of 1984 year-class fish in Cranberry using same gear), it appeared that the gillnets were sampling the more active, faster growing members of the cohort in Woods Lake. The low metabolic levels and growth efficiency estimated for the larger fraction of this group, not sampled by the gillnets, could have resulted from lower activity and isolation at deeper levels in the lake where lower temperatures, lower pH, and less food occurred. Although deep water netting was not conducted to confirm this hypothesis, sonar surveys made during August, 1985 revealed high concentrations of fish just below the thermocline in the deepest part of the Woods Lake basin (Brandt and Unger 1986). The tendency for this strain to seek lower temperatures (Cone 1987) and the observations from this and other studies (Webster and Flick 1981) of relatively higher overwinter growth rates lends some support to the hypothesized behavior and distribution of these fish.

The marked reductions in growth efficiency and ration intake by the 1985 cohort in Cranberry Pond during the winter of 1985 reflect the effects of acidification induced stress described previously. The decreased metabolic level of these fish, compared with the same cohort in Woods Lake (Fig. 6), is also indicative of physiological stress. Decreased growth efficiency of the 1985 year-class in Woods Lake during the summer of 1986 was associated with reduced food consumption rates of smaller invertebrates (Gloss et al. 1989).

## General Discussion

Mean annual biomass and total production of brook trout in Woods Lake and Cranberry Pond (Table 7), for the first year following liming and initial stocking, were similar to levels observed in other limed and circumneutral lakes in the Adiron-

TABLE 7. Mean annual biomass ($\bar{B}$), total fish production ($P$), and estimated total food consumption ($R$) for Spring–Spring and Fall–Fall periods in Woods Lake and Cranberry Pond.

| Lake | Period | $\bar{B}$(kg·ha$^{-1}$) | $P$(kg·ha$^{-1}$·yr$^{-1}$) | $R$(1000 kcal·ha$^{-1}$·yr$^{-1}$) | $P/B$ | $P/R$ |
|---|---|---|---|---|---|---|
| Woods Lake | 6/85–5/86 | 7.7 | 10.2 | 41.3 | 1.3 | 0.25 |
| Cranberry Pond | 6/85–5/86 | 9.8 | 13.6 | 51.4 | 1.4 | 0.26 |
| Woods Lake | 10/85–9/86 | 6.9 | 9.8 | 40.3 | 1.4 | 0.24 |
| Cranberry Pond | 10/85–9/86 | 4.4 | 1.8 | 9.7 | 0.4 | 0.19 |

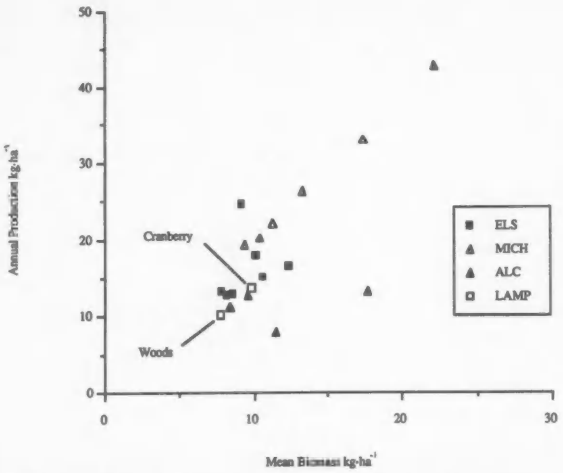


FIG. 7. Mean annual biomass and total annual production of stocked brook trout in limed (ELS) and circumneutral (ALC) Adirondack and Michigan Lakes (MICH) compared with levels in the LAMP study lakes. Data presented are for first year after stocking in all waters.

dack region (Fig. 7). All of the extensive liming study (ELS) limed lakes (Schofield et al. 1986) were stocked with fall fingerling Domestic × Temiscamie strain brook trout obtained from the same stocks utilized in the LAMP study. Both wild and domestic strains were represented in the circumneutral Adirondack league club (ALC) lakes studied by Hatch and Webster (1961). Collectively, these oligotrophic waters appear to support rather limited brook trout standing crops of 10–20 $kg \cdot ha^{-1}$ at production levels of 7–16 $kg \cdot ha^{-1} \cdot yr^{-1}$. Standing crops of brook trout reported for dilute lakes in Ontario (Fraser 1981) are comparable with those observed in the Adirondack region. A much wider range of biomass and production was reported by Gowing (1986) for relatively hard water lakes in Michigan that were stocked with fall fingerling Assinica strain brook trout (Fig. 7). This variability in production was attributed to inherent differences in productivity of these lakes and the effects of rotenone treatment on the invertebrate forage base on one lake exhibiting the lowest levels of production and biomass.

Ratios of production to mean biomass (*P/B*) in Woods Lake and Cranberry Pond (Table 7) were at the low end of the range observed for limed lakes in the ELS study (*P/B* 1.3–2.6), but approximately the same as levels reported for the four circumneutral lakes studied by Hatch and Webster (1961). Chapman (1967) noted that the relatively narrow range of *P/B* ratios observed for a diverse range of fish species populations, representing both high and low productivity systems (including the Adirondack lakes), probably reflects the effects of natural controls on biomass that are conducive to rapid tissue elaboration by the populations. Hatch and Webster (1961) and Schofield et al. (1986) observed declines in brook trout biomass after standing crops reached peak levels of 15–20 $kg \cdot ha^{-1}$. The former authors recommended management of these lakes for spring standing crops of 11–14 $kg \cdot ha^{-1}$ to achieve optimal angling yields. Maintenance of these levels could be simply regulated by controls of angling harvest and recruitment (via stocking and/or manipulation of natural reproduction), providing that the forage base remains stable. The latter caveat is particularly relevant to limed systems that appear to exhibit considerable instability in the structure of the prey communities as a result of both marked perturbations in water chemistry and the sudden alteration in predation pressure resulting from the reintroduction of fish (Gloss et al. 1989; Schaffner 1989; Evans 1989).

Based on the results of this study and others involving reintroductions of fish following liming (Schofield et al. 1986), stocked salmonid populations appear to rapidly (within 1–2 yr) attain levels of biomass and production comparable with, or in some cases even higher than, levels observed in circumneutral lakes that have established predator–prey equilibria over longer periods. However, these relatively short-term observations of increased production and biomass in the limed lakes should not be misconstrued as representative of equilibrium conditions. Based on an average caloric content of 500 cal·g wet weight for invertebrate forage taxa, the estimated ration levels necessary to maintain these levels of biomass and production in the LAMP study lakes were on the order of 80–100 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Table 7). This level of predation probably exceeded the potential production of larger, more desirable prey taxa present prior to the introduction of fish (Evans 1989) and was likely responsible for the rapid depletion of these prey populations that was observed during the first year following the introduction of fish (Gloss et al. 1989; Schaffner 1989). The primary initial consequence of the resulting decrease in mean size of available prey, relative to the concurrent increased mean size of the trout, was decreased growth efficiency. However, decreased survival and growth resulting from adverse physical–chemical conditions (temperature–pH gradient in Woods Lake and reacidification of Cranberry Pond) in these lakes during the first year after stocking appeared to be of greater significance than food limitation in regulating production and biomass. Predation influenced alterations of the size structure of the invertebrate prey resource in Woods Lake will likely be of greater importance in determining maximum attainable size and total production by the trout population in the future.

## Acknowledgments

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# Response of Limnetic Insect Populations of Two Acidic, Fishless Lakes to Liming and Brook Trout (*Salvelinus fontinalis*)[1]

Richard A. Evans

*Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, NY 14853, USA*

Evans, R. A. 1989. Response of limnetic insect populations of two acidic, fishless lakes to liming and brook trout (*Salvelinus fontinalis*) introduction. 46: 342–351.

Seasonal population density estimates of limnetic insects in two Adirondack (New York) lakes were obtained from horizontal and vertical net tows and benthic sweep net samples over a 3-yr period; 1 yr while the lakes were acidic and fishless, and 2 yr following addition of (calcium carbonate) $CaCO_3$ and the introduction of brook trout (*Salvelinus fontinalis*). Before treatment, the limnetic insect assemblages in the study lakes resembled those reported from acidic and/or fishless lakes in Sweden and Canada. Maximum densities of dominant taxa were: Notonectidae; $1.5 \cdot m^{-3}$; Corixidae; $1.1 \cdot m^{-3}$, *Graphoderus* (Dytiscidae) larvae; $0.27 \cdot m^{-3}$; and *Chaoborus americanus*; $400 \cdot m^{-3}$. Within 3 mo after treatment, all limnetic populations were near or below the detection limit ($0.01 \cdot m^{-3}$). Limnetic densities of notonectids, corixids, and *C. americanus* were significantly lower (Mann–Whitney U-tests), and benthic densities of Hemiptera and Coleoptera tended to be lower (sign tests) the summer after treatment than the previous summer. Calculated trout predation levels on Hemiptera and *C. americanus*, and evidence from the literature, strongly suggest that predation was the major cause of reduced limnetic insect populations. The rapid reduction or elimination of these populations indicates considerable instability of the predator–prey relationships of acidic lakes which have been recently limed and stocked with fish.

On a fait des estimations saisonnières de la densité des populations d'insectes limnétiques dans deux lacs des Adirondacks (État de New York) d'après des échantillons prélevés au filet à l'horizontale et à la verticale et à la drège en zone benthique sur une période de 3 an, soit 1 an où les lacs étaient acidifiés et ne contenaient pas de poissons et 2 an après un traitement au (calcium carbonate) $CaCO_3$ et l'ensemencement d'ombles de fontaine (*Salvelinus fontinalis*). Avant le traitement, les groupements d'insectes limnétiques dans les lacs étudiés ressemblaient à ceux de lacs acidifiés ou dépourvus de poissons signalés en Suède et au Canada. On a déterminé la densité maximale des taxons dominants : notonectidés : $1{,}5 \cdot m^{-3}$; corixidés : $1{,}1 \cdot m^{-3}$; larves de *Graphoderus* (dytiscidés) : $0{,}27 \cdot m^{-3}$; *Chaoborus americanus* : $400 \cdot m^{-3}$. Trois mois après le traitement, toutes les populations limnétiques étaient sous la limite de détection ($0{,}01 \cdot m^{-3}$) ou en approchaient. L'été suivant le traitement, la densité des populations limnétiques de notonecdités, corixidés et *C. americanus* avait baissé dans une mesure significative (tests U de Mann–Whitney) et celle des populations benthiques d'hémiptères et de colépotères tendait à être faibles (tests des signes) par comparaison à l'été précédent. On a calculé l'intensité de la prédation des hémiptères et de *C. americanus* par les ombles et d'après les résultats de ces calculs et les données présentées à ce sujet dans la littérature, il est très vraisemblable que la prédation ait été la principale cause de la réduction des populations d'insectes limnétiques. Étant donné la rapidité de la réduction ou de l'élimination de ces populations, les relations prédateur–proie se caractériseraient par une considérable instabilité dans les lacs acidifiés récemment traités au calcaire et ensemencés de poissons d'élevage.

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Lake acidification can cause changes in aquatic insect assemblages through both direct and indirect mechanisms. Reductions or eliminations of plant and animal populations, caused by direct physiological stress, can in turn alter habitat characteristics and both competetive and predator–prey relationships in acidified lakes (Eriksson et al. 1980; Haines 1981; Henrikson and Oscarson 1981; Nilssen et al. 1984; Havas 1985; Schindler et al. 1985; Okland and Okland 1986). In particular, the absence of insectivorous fish in acidified lakes may result in the appearance and/or increased populations of insect taxa that are acid tolerant but susceptible to fish predation. A field experiment in Sweden (Henrikson and Oscarson 1978b) demonstrated that perch (*Perca fluviatilis*) predation can limit the distribution and abundance of the corixid *Glaenocorisa propinqua* independently of acidity. Other studies have shown that *G. propinqua* occurred in 86% of acidified, fishless lakes surveyed in Sweden (Henrikson and Oscarson 1981), and that relatively dense populations of corixids and dytiscids exist in the limnetic zones of these lakes (Henrikson and Oscarson 1984, 1985). The fact that limnetic insect populations have been found to increase after liming without fish introduction (Henrikson and Oscarson 1984) suggests that their relative abundance in acidified, fishless lakes is primarily a result of the lack of fish predators, rather than the acidic environment per se.

In Canada, Bendell (1986) and Bendell and McNicol (1987) found from lake surveys that, independent of acidity, fishless lakes supported similar aquatic insect assemblages characterized by an abundance of Notonectidae, Corixidae, *Graphoderous liberus* (Coleoptera; Dytisidae), and *Chaoborus ameri-*

[1]This is a part of a series of 13 papers devoted to the Lake Acidification Mitigation Project.

*canus* (Diptera; Chaoboridae). They concluded that fish predation is the most important factor structuring assemblages of nektonic insects. However, in contrast with the Swedish studies, these studies did not sample the limnetic zone but were restricted to water less than 1 m deep near the shore.

Lake liming has been used extensively in Sweden (Lindstrom et al. 1984; Lessmark and Thornelof 1986), and is currently being developed in the U.S. (Schreiber and Britt 1987; Porcella 1989) to restore fish populations to acidified lakes. Abundant populations of limnetic insects could significantly contribute to the growth and production of fish in recently limed lakes, at least temporarily. But if liming and fish introductions eliminate energetically important prey populations before other prey populations invade and/or sufficiently increase, the growth and production of fish in these lakes may decline markedly over time. However, the response of limnetic insect populations to both liming and fish introduction has not been documented in previous liming and fish introduction studies (Hultberg and Andersson 1982; Hasselrot et al. 1984; Booth et al. 1986).

In the Adirondack Mountains of New York, it has been estimated that fish populations have been eliminated from several hundred lakes as a result of acidification (Schofield 1976; Haines and Baker 1986). The present study was undertaken as part of the Lake Acidification Mitigation Project (LAMP) (Porcella 1989) to: (a) provide a quantitative description of the limnetic insect populations of two acidified, fishless, Adirondack lakes; (b) evaluate the hypothesis that limnetic insect populations significantly decline following liming and introduction of brook trout (*Salvelinus fontinalis*); (c) provide evidence for the possible mechanisms causing any observed population changes of limnetic insects.

## Materials and Methods

### Study Sites

Woods Lake (23 ha; $Z_{mean}$ = 3.5 m; $Z_{max}$ = 12 m) and Cranberry Pond (8 ha; $Z_{mean}$ = 2.9 m; $Z_{max}$ = 7.6 m) are located in adjacent watersheds at about 600 m elevation in the Adirondack Park of New York (Staubitz and Zarriello 1989). Both lakes have recently become acidified and fishless, although each had historically supported brook trout populations (Gloss et al. 1987). A calcium carbonate ($CaCO_3$) slurry was applied to Woods Lake on 30 May 1985 and to Cranberry Pond on 31 May 1985 (Porcella 1989). In both lakes $CaCO_3$ addition produced large, immediate increases in dissolved calcium, acid neutralizing capacity (ANC), and dissolved inorganic carbon (DIC); pH increased from values below 5 to above 9, but declined to values below 8 within 3 wk (Fordham and Driscoll 1989). Cranberry Pond reacidified (ANC = 0 $\mu eq \cdot L^{-1}$; pH = 5) within 6 mo (November 1985) after treatment, whereas Woods Lake maintained circumneutral conditions (ANC > 40 $\mu eq \cdot L^{-1}$; pH > 6) throughout this study (Driscoll et al. 1989).

Two thousand four hundred fingerling and 538 adult brook trout were stocked into Woods Lake in the fall (Nov. 19–20, 1984) before it was limed, but fewer than 300 of these fish survived through April 1985 (Gloss et al. 1987). Five thousand fingerling and 1200 yearling brook trout were stocked into Woods Lake, and 2000 fingerling and 400 yearling brook trout were stocked into Cranberry Pond June 2–5, 1985 (Gloss et al. 1989). Data from Gloss et al. (1989) indicate that by May 1986, brook trout densities in Woods Lake declined from a stocking level of about 270 fish$\cdot ha^{-1}$ to less than 100 fish$\cdot ha^{-1}$. Brook trout densities in Cranberry Pond declined much more dramatically over this time period, from a stocking level of about 300 fish$\cdot ha^{-1}$ to less than 10 fish$\cdot ha^{-1}$.

### Insect Sampling and Processing

Insect population densities were estimated by three different methods, each of which sampled a different region of the lakes. Estimates of daytime densities of *Chaoborus* larvae and pupae throughout the water column were obtained from zooplankton samples collected by towing a 30-cm diameter, 80-$\mu$m mesh net vertically from 1 m above the substrate to the surface (Schaffner 1989). Duplicate tows were taken at three stations in Cranberry Pond and four stations in Woods Lake at approximately 3-wk intervals from January 1984 through October 1986 (Schaffner 1989).

To estimate densities of insects inhabiting the near-surface layer of open water, a 75-cm diameter, 1-mm mesh Nitex net equipped with a mechanical flow meter (Model 2030C, General Oceanics, Miami, FL) was towed horizontally through the upper 1 m of water behind a small powerboat. The boat was steered in zigzag paths such that the net was rarely in the boat's outwash. Practical constraints limited horizontal sampling to the upper 1 m of water. Although the 1-mm mesh did not retain first and second instar *Chaoborus* larvae, it was chosen to efficiently capture larger instars and insects by minimizing friction between the net and water and thus minimizing pressure wave formation. Henrikson and Oscarson (1978a, 1981, and 1985) also used 1-mm mesh for quantitatively sampling air-breathing aquatic insects. Horizontal samples were taken in Woods Lake and Cranberry Pond during late morning or early afternoon in July, August, and September (also November in Woods Lake) 1984, and May through October 1985 and 1986. Samples were collected from central midlake stations in both lakes and from a nearshore station about 10 m from the shoreline at Woods Lake. On most sample dates three tows were taken at each station, but during September and October 1985 and October 1986 only two were taken. A total of 36 horizontal tows were taken from Woods Lake before treatment, and 72 after treatment. Fifteen horizontal tows were taken from Cranberry Pond before treatment, and 36 after treatment. The sampling method allowed the rapid collection of large volume samples to detect low population densities; the length of time to collect each sample ranged from 2 to 4 min, and the velocity of water flowing through the net ranged from 3.5 to 7 km$\cdot h^{-1}$ (which is at least three times the maximum swimming speed measured for a corixid (Crisp 1962)). The volume of water filtered by each sample ranged from 50 to 235 $m^3$; thus the minimum population densities detectable in each tow were between 0.02 and 0.005 individual$\cdot m^{-3}$.

Densities of limnetic insects utilizing benthic areas were estimated from benthic samples collected with a D-frame, 1-mm mesh sweep net while snorkeling. Six transects running perpendicular to the prevailing depth contours were established in each lake using a random number table. Benthic samples, each covering 0.48 $m^2$, were taken at four discreet depths at each transect: 0.5, 1.5, 3.0, and 4.5 m. Samples were collected every 3 or 4 wk in each lake, from early July 1984 through late August 1986, during ice-free periods. However, only those data which are presently available from samples taken at similar dates before and after liming (both July and August of 1984 and 1985) are considered here.

TABLE 1. Maximum densities (number per cubic metre) of aquatic insect taxa in limnetic samples from Woods Lake and Cranberry Pond 1984–86.

| Taxa | | | | Maximum No.·m$^{-3}$ | |
|---|---|---|---|---|---|
| Order | Family | Genus | Species | Woods Lake | Cranberry Pond |
| Hemiptera | Notonectidae | *Notonecta* | *insulata, undulata* | 0.16 | 0.32 |
| | | *Buenoa* | *margaritacea* | 1.50 | 1.40 |
| | Corixidae | *Dasycorixa* | | 1.13 | 0.18 |
| | | *Hesperocorixa* | | 0.04 | 0.06 |
| Diptera | Chaoboridae | *Chaoborus* | *americanus* | — | 400 |
| | | *Chaoborus* | *punctipennis* | 175[a] | — |
| Coleoptera | Dytiscidae | *Graphoderus* | | 0.05 | 0.27 |
| | | *Laccophilus* | | | — |
| | Gyrinidae | *Gyrinus* | | 0.01 | 0.01 |
| | | *Dineutus* | | 0.11 | — |
| | | | | 0.10 | |
| Trichoptera | Leptoceridae | *Triaenodes* | | 0.01 | 0.04 |
| Odonata | Coenagrionidae | *Enallagma* | | 0.02 | 0.02 |

[a]*C. punctipennnis* density from nighttime vertical tows with a 50-cm diameter, 153-μm mesh net (M. Robbins, Department of Biology, Indiana University, Bloomington, IN, pers. comm.).

All insects were preserved in the field; those collected by horizontal tows and benthic sweeps were preserved in 70% EtOH (ethanol) whereas *Chaoborus* from zooplankton tows were preserved in 4% formaldehyde. Keys by Peckarsky et al. (1989), and Merritt and Cummins (1984) were used to identify insects to genus. Species of *Chaoborus* were identified according to Saether (1972). When more than 500 *C. americanus* were in a sample, it was mixed in 4 L of 70% EtOH and nine 60-mL subsamples were taken (with replacement). In such cases a two-stage sampling formula (Cochran 1977) was used to calculate variances. Because the size structure of insect populations can be used to interpret possible mechanisms of population changes, lengths of insects were measured to the nearest 0.1 mm using an ocular micrometer.

## Results and Discussion

### Taxonomic Composition and Population Densities

Notonectidae and Corixidae (Hemiptera), Chaoboridae (Diptera), Dytiscidae (Coleoptera), and other insects populated the limnetic regions of Woods Lake and Cranberry Pond (Table 1). Maximum densities of all taxa, except for *C. punctipennis* in Woods Lake and corixids and early instar *C. americanus* in Cranberry Pond, were observed during the pretreatment period. In Woods Lake, the maximum notonectid density(1.5·m$^{-3}$; 80% CI, 1.17–1.9·m$^{-3}$) and corixid density (1.1·m$^{-3}$; 80% CI; 0.77–1.43·m$^{-3}$) were observed at the nearshore station in late August 1984 (Fig. 1). *Chaoborus punctipennis* was found in Woods Lake at densities up to 175·m$^{-3}$ in vertical tows taken at night (M. Robbins, Department of Biology, Indiana University, Bloomington, Indiana, 47405, pers. comm.) and over 50·m$^{-2}$ in daytime benthic samples (R. A. Evans, unpubl. data) but was absent from daytime horizontal tow samples. This species is known to inhabit the metalimnion or hypolimnion during the day and migrate to the epilimnion at night (Carter and Kwik 1977).

In Cranberry Pond the highest notonectid density (1.4·m$^{-3}$; 80% CI, 1.23–1.57·m$^{-3}$) was observed on the first sampling date, in July 1984 (Fig. 2). Corixid densities in Cranberry Pond, in contrast, peaked at about 0.35·m$^{-3}$ (80% CI, 0.29–0.51·m$^{-3}$) about a month following treatment in 1985 (Fig. 2). While densities of third and fourth instar *C. americanus* peaked at about 200·m$^{-3}$ (80% CI, 175–225·m$^{-3}$) in early May 1985, before treatment (Fig. 2), first and second instar densities reached about 400·m$^{-3}$ (80% CI, 80–720·m$^{-3}$) in early June, 1 wk after treatment (Fig. 3A).

*Graphoderus* (Coleoptera: Dytiscidae) larvae were found in densities of 0.27·m$^{-3}$ (SD = 0.08·m$^{-3}$) in Cranberry Pond and 0.05·m$^{-3}$ (SD = 0.04·m$^{-3}$) in Woods Lake on the first sampling date, but at much lower densities thereafter. Visual observations made while snorkeling indicated that limnetic populations of *Graphoderus* larvae had been much greater in both lakes during June and early July of 1984, before limnetic sampling began, than afterward.

Two notonectid genera, *Buenoa* and *Notonecta*, and two corixid genera, *Dasycorxia* and *Hespercorixa*, occurred in both study lakes. *Buenoa* accounted for about 95% of the notonectid populations in late August and September 1984. *Notonecta* however accounted for at least 75% of the July 1984 Woods Lake notonectid populations and the 1985 populations of both lakes. *Dasycorixa* was at least 10-fold more abundant than *Hespercorixa* in Woods Lake, but in Cranberry Pond *Hespercorixa* sometimes accounted for nearly 50% of the corixids.

Within 2 mo after liming and brook trout introduction, notonectid, corixid, and *C. americanus* populations declined to levels near or below detection limits (<0.01 individuals·m$^{-3}$), and were extinct or remained below detection limits through the fall of 1985 (Fig. 1, 2, and 3). Notonectid populations in Woods Lake were extinct or continued below detection limits throughout the ice-free period of 1986 (Fig. 1A), as did the *C. americanus* population in Cranberry Pond (Fig. 2). However, corixids (both *Dasycorixa* and *Hesperocorixa*) were collected in nearshore samples of Woods Lake in 1986 (Fig. 1B). Corixids (mostly *Dasycorixa*), and to a lesser extent notonectids (mostly *Notonecta*) in Cranberry Pond increased somewhat during 1986 (Fig. 2), after the pond had reacidified (Driscoll et al. 1989) and the brook trout population had declined to fewer than 10·fish·ha$^{-1}$ (Gloss et al. 1989).

To determine if limnetic insect densities within each lake were significantly different between periods before and after treatment, Mann–Whitney U-tests were performed. Comparisons were restricted to similar dates between years.

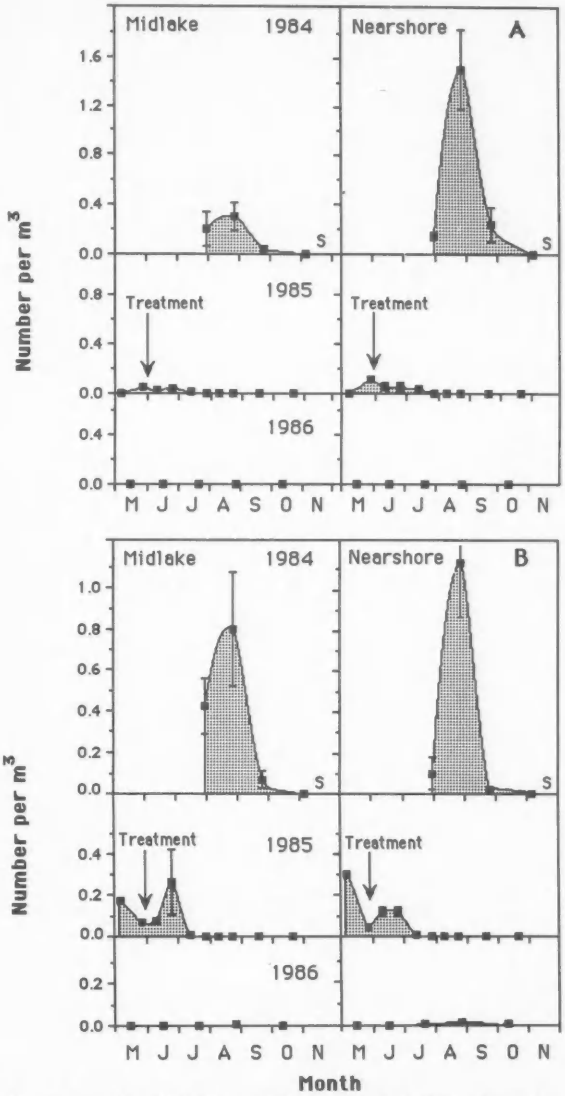


FIG. 1. Densities of (A) Notonectidae and (B) Corixidae in the surface layer of midlake and near shore regions of Woods Lake 1984–86. Error bars represent one standard deviation. *S* indicates stocking of brook trout, and arrows indicate treatment of liming and introducing brook trout.

Samples from two or more consecutive dates within years were pooled, and thus treated as replicates, to reduce the number of comparisons. Because a population's size at a given time is theoretically dependent on its size at a preceeding time, this pooling of samples from different dates violates the assumption of independence within a sample. However, no statistical analysis was found which would avoid this problem, given the limited time series data available.

One-tailed Mann–Whitney U-tests indicated that *C. americanus* in Cranberry Pond, and notonectids and corixids in both lakes, were significantly less abundant after treatment (late July through October) in 1985 than in 1984 (each $p <$ 0.05). Furthermore, posttreatment notonectid and corixid

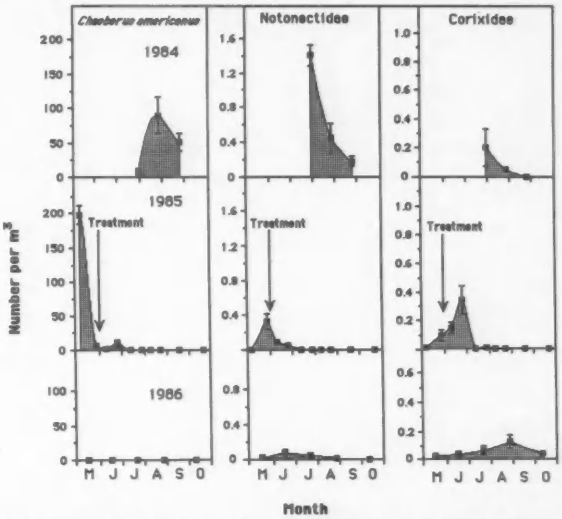


FIG. 2. Densities of *C. americanus*, Notonectidae, and Corixidae in the surface layer of Cranberry Pond 1984–86. Error bars represent one standard deviation, and arrows indicate treatment of liming and introducing brook trout.

populations in Cranberry Pond were significantly larger (June through October) in 1986 than in 1985 (each $p < 0.05$). No statistical comparisons were made of population densities immediately before and after treatment in 1985 because of the confounding influence of life cycle events. For example, Fig. 3B indicates that *C. americanus* overwintered as fourth instars (8–11 mm total body length), pupated and emerged in May, and reappeared as first and second instars (2–4 mm total body length) in early June (Fedorenko and Swift 1972; Carter and Kwik 1977). Thus the population density of late instar *C. americanus* dropped from about 200 to $10 \cdot m^{-3}$ just before Cranberry Pond was limed (Fig. 2), whereas the population density of early instars increased dramatically over this same period (Figure 3A).

Benthic densities of hemipterans in the study lakes were significantly lower (sign tests) during July and August the year after treatment than during July and August of the previous year (Table 2). In Cranberry Pond however, the differences were not significant at $a = 0.05$ ($p = 0.0625$). Benthic densities of Dytiscid and Gyrinid larvae in Woods Lake (not shown) were significantly lower in July 1985 than in July 1984 (sign test; $n = 19$, $p << 0.05$).

## Recruitment

Since population changes during any given period are determined by the relative rates of birth and death (assuming no immigration or emmigration), explanations (as opposed to descriptions) of population change must necessarily begin by identifying whether or not births (or recruitment), as well as deaths, occurred. To identify the relative magnitudes and periods of recruitment into limnetic insect populations, length–frequency histograms were constructed. Histograms were considered reliable and useful only for those genera for which at least 20 individuals could be measured on each of at least three different dates.

Recruitment of *Dasycorixa* in Woods Lake was evident when sampling began in July 1984, and continued through August,

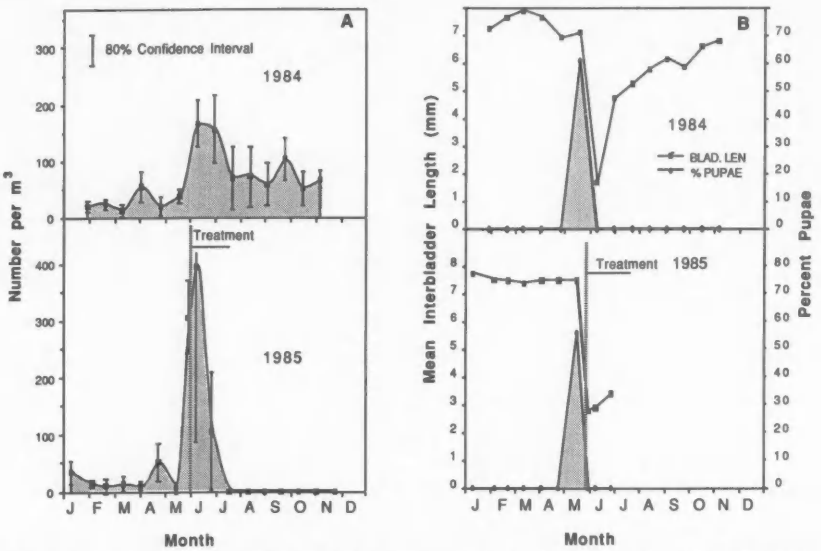


FIG. 3. (A) *C. americanus* densities estimated from vertical zooplankton tows in 1984 and 1985 in Cranberry Pond. Error bars represent 80% confidence intervals for the means. (B) Mean interbladder length and percent pupae of *C. americanus* specimens in zooplankton tows.

TABLE 2. Mean densities (number per square metre) of Hemiptera (Corixidae and Notonectidae) determined from benthic sweep net samples in Woods Lake and Cranberry Pond, and sign test results from density estimates paired by sample location (depth and transect) and date (before and after treatment). $n$ is the number of nonties (out of 24 pairs), $T$ is the number of pairs in which hemipteran density was greater in 1985 than in 1984, and $p$ is the probability of obtaining a value of $T$ as small or smaller than than observed.

| | | Depth (m) | | | | Sign test | | |
|---|---|---|---|---|---|---|---|---|
| Lake | Date | 0.5 | 1.5 | 3.0 | 4.5 | $n$ | $T$ | $p$ |
| Cranberry Pond | 24 July 1984 | 3.1 | 0.7 | 0 | 0.7 | | | |
| | 25 July 1985 | 1.7 | 0.3 | 0.3 | 0 | 7 | 1 | 0.0625 |
| Woods Lake | 27 July 1984 | 4.9 | 2.1 | 1.0 | 0 | | | |
| | 26 July 1985 | 0.7 | 0 | 0 | 0 | 7 | 0 | 0.0078 |
| | 21 Aug. 1984 | 1.0 | 5.2 | 0.7 | 1.0 | | | |
| | 22 Aug. 1985 | 0.7 | 0.3 | 0 | 0 | 11 | 2 | 0.0327 |

but had ended before late September (Fig. 4). In 1985, *Dasycorixa* recruitment in both lakes had begun by late May and continued through June (Fig. 4 and 5), after which time the populations declined to levels below detection. *Notonecta* recruitment had also begun by late May 1985 in both lakes (Fig. 4 and 5), but whereas growth of new individuals was apparent in the Cranberry Pond population during June 1985, no such growth was apparent in the Woods Lake *Notonecta* population. *Buenoa* recruitment occurred in both lakes before sampling began in 1984 (the only year for which sufficient data were available to construct reliable histograms), and growth to over-wintering (adult) size was completed by late September (Fig. 6).

## Brook Trout Predation Levels

Brook trout predation levels on *C. americanus* and Hemiptera over certain time periods were calculated to indicate the impact trout predation may have had on these insect populations. Two different predation levels were calculated by using the model-derived brook trout rations from Schofield et al. (1989) and empirical stomach content data from Gloss et al. (1989). One predation estimate was obtained by multiplying a model-derived estimate of the biomass of a particular prey taxon consumed by brook trout (prey specific ration) over a given period (Schofield et al. 1989) by the number of that particular prey per unit biomass, to arrive at the number of prey consumed over the period. The second predation estimate was obtained by multiplying a model-derived estimate of the total prey biomass consumed by brook trout (total ration) over a given period (Schofield et al. 1989) by an empirical estimate of the fraction of the diet contributed by a particular prey taxon over the period (Gloss et al. 1989); the result was then converted from biomass units to numbers as above. The predation estimates were then compared with the prey densities present at the start of the period (initial) and the prey densities present in late June (when the first brook trout stomach samples were collected) to indicate

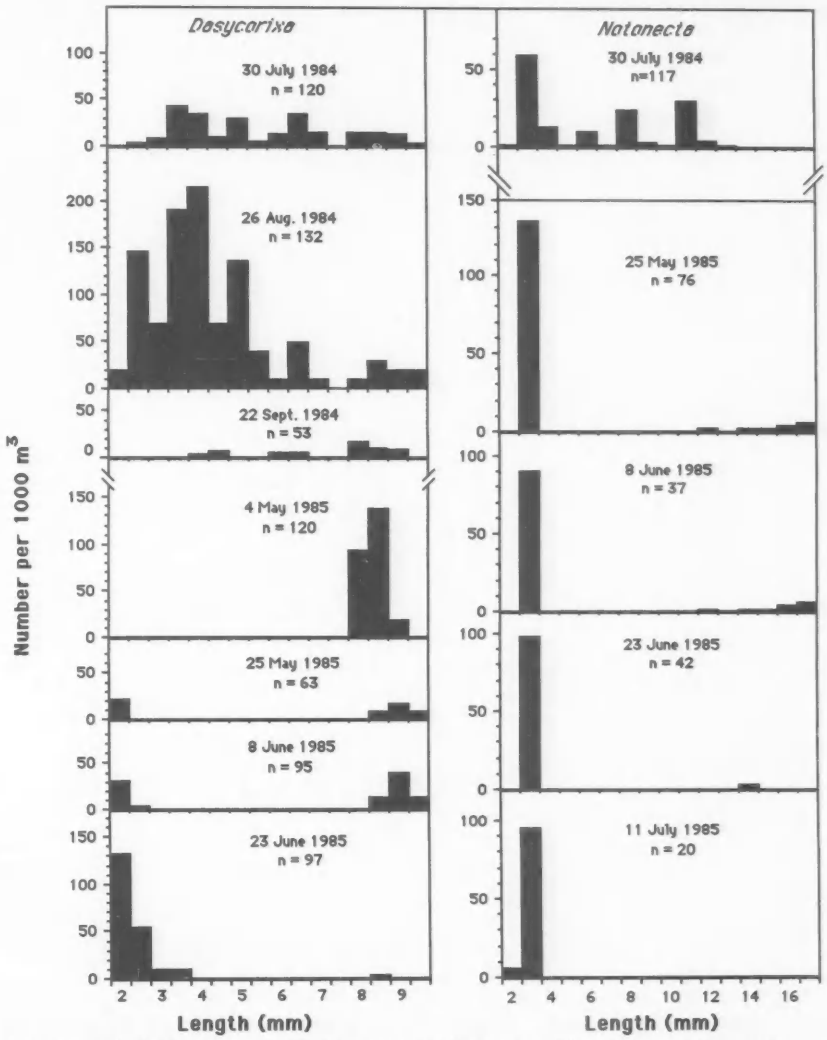


FIG. 4. Length–density histograms for *Dasycorixa* and *Notonecta* in Woods Lake. *n* indicates the number of specimens measured from a given date.

the impact trout predation may have had on limnetic insect populations.

Predation levels calculated by either method exceeded the estimated initial and also late June densities of Hemiptera in both lakes (Table 3). These predation levels may not be unrealistic, since recruitment into the Hemiptera populations of both lakes was occurring throughout the periods considered (Fig. 4 and 5). Also, they may not be unrealistic because the initial densities obtained from horizontal tows do not represent whole-lake densities, but only those of the upper 1 m of limnetic water. Since littoral (vegetated) regions probably supported higher Hemipteran densities per unit volume than limnetic regions (Henrikson and Oscarson 1985; Bennett and Streams 1986), the measured densities probably underestimated whole-lake densities. In any case the results indicate that if brook trout foraged in the limnetic zones of the lakes at all, and possibly even if they did not, predation would account for the virtual elimination of limnetic populations of Hemipterans.

The predation level on *C. americanus* in Cranberry Pond calculated strictly from the model was much greater than that calculated from gut content data (Table 3); the latter probably underestimated the actual predation considerably for at least two reasons. First, only the stomach contents of trout >200 mm were determined (Gloss et al. 1989), even though fish in this size class represented only about one sixth of the total population; most trout were smaller than this. If the rations of smaller fish included even a slightly higher proportion of *C. americanus* than those of the larger, sampled fish, the calculated predation level would be biased low. Second, trout gut contents were first sampled at the end of June 1985, nearly a month after the trout were stocked. During this period *C. americanus* densities declined dramatically (Fig. 3A); the lowered densities in the lake would presumably result in lowered consumption rates by brook trout, and hence a smaller portion of the gut contents, compared with earlier in the month. Nevertheless, the predation estimate based on gut contents indicates

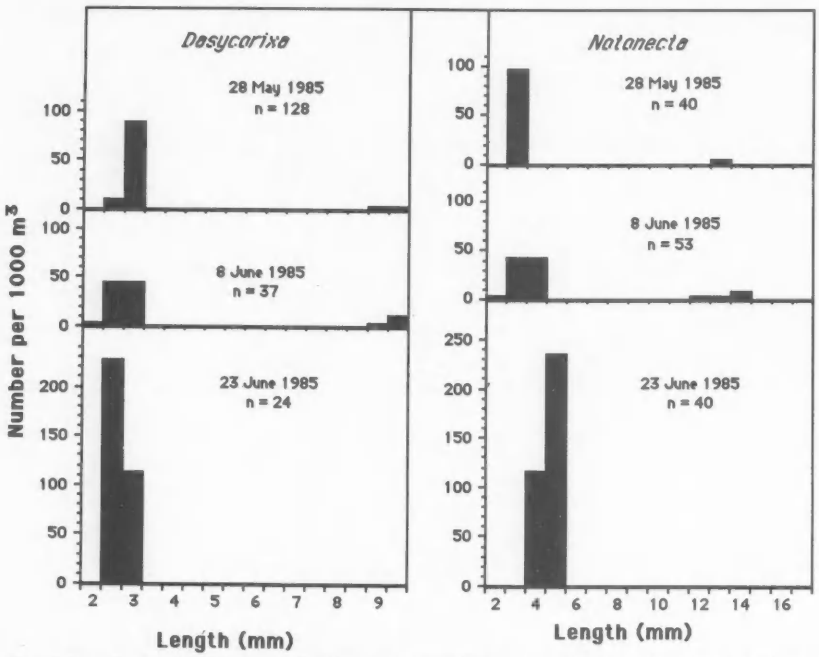


FIG. 5. Length–density histograms for *Dasycorixa* and *Notonecta* in Cranberry Pond. *n* indicates the number of specimens measured from a given date.

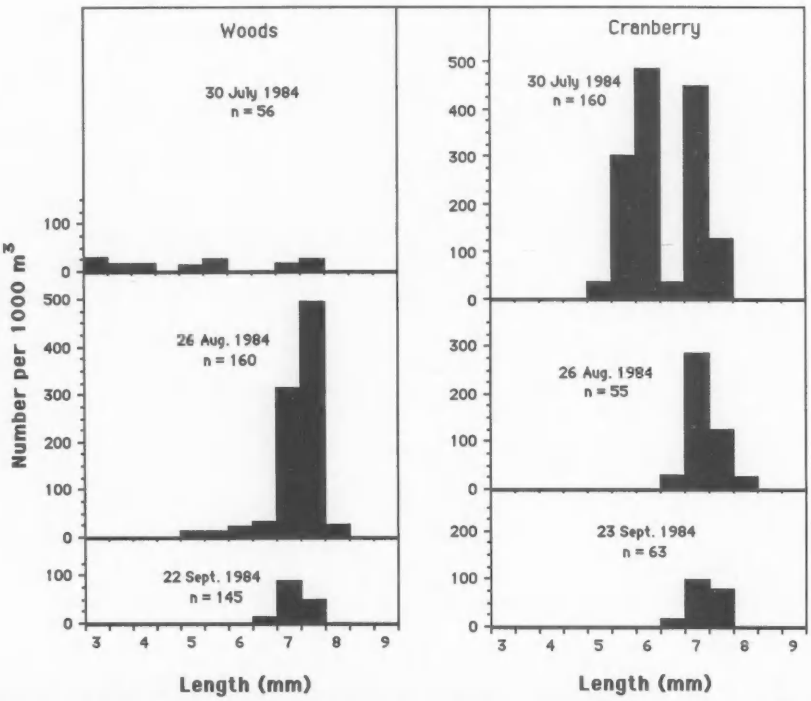


FIG. 6. Length–density histograms for *Buenoa* in Woods Lake and Cranberry Pond. *n* indicates the number of specimens measured from a given date.

TABLE 3. Brook trout predation levels (cumulative) and population densities of, *C. americanus* and Hemiptera (Corixidae and Notonectidae) June through October.

| Lake | Year | Taxon | Predation[a] (No.·m$^{-3}$) | Predation[b] (No.·m$^{-3}$) | Initial No.·m$^{-3}$ | Late June No.·m$^{-3}$ |
|---|---|---|---|---|---|---|
| Cranberry Pond | 1985 | *C. americanus* | 220 | 43 | 400 | 100 |
| Cranberry Pond | 1985 | Hemiptera | 8.4 | 5.1 | 0.4 | 0.4 |
| Woods Lake | 1985 | Hemiptera | 2.3 | 1.7 | 0.2 | 0.4 |
| Woods Lake | 1986 | Hemiptera | 1.1 | 5.8 | 0.0 | 0.0 |

[a]Predation calculated from the model of Schofield et al. (1989).
[b]Predation calculated from a combination of the model of Schofield et al. (1989) and monthly gut content analysis (Gloss et al. 1989).

that within 5 mo trout predation eliminated almost one half of the *C. americanus* population present at the time stomach samples were first taken. This agrees well with the modelled estimate, which indicates that within 5 mo trout eliminated at least one half of the *C. americanus* population present initially. It should be noted that *C. americanus* recruitment, in contrast with that of the Hemiptera, ended very soon after the time of treatment (Fig. 3B). Therefore any *C. americanus* deaths caused by trout predation could not be replaced by new recruitment.

## General Discussion

Prior to treatment, Woods Lake and Cranberry Pond supported populations of limnetic insects similar to those reported from acidified, fishless lakes in Scandinavia (Eriksson et al. 1980), and similar to the littoral assemblages of nectonic insects inhabiting fishless lakes in Canada (Bendell and McNicol 1987). In general, significant populations of hemipterans, dytiscid larvae, and various *Chaoborus* species were common in all of these lakes. One difference however is that notonectids were relatively abundant in the Adirondack lakes studied here and in the Canadian lakes surveyed by Bendell and McNicol (1987), but have not been reported in the Scandinavian lakes (Eriksson et al. 1980; Henrikson and Oscarson 1981).

The major difference between the limnetic insect assemblages in the two study lakes prior to treatment was the presence of *C. punctipennis* and absence of *C. americanus* in Woods Lake, in contrast to the presence of *C. americanus* and absence of *C. punctipennis*, even in vertical nighttime tows (M. Robbins, Department of Biology, Indiana University, Bloomington, IN, pers. comm.) in Cranberry Pond. Several factors have probably caused this difference. Surveys (Pope et al. 1973; Von Ende 1978, 1979, 1981; Carter et al. 1980; Borkent 1981) have shown that, as in the study lakes, *C. americanus* and *C. punctipennis* do not occur sympatrically. These surveys also suggest that fish predation limits the distribution of *C. americanus* but not *C. punctipennis* because *C. americanus* has been found only in fishless lakes, whereas *C. punctipennis* has been found primarily in lakes having fish. This hypothesis has been supported by field experiments (Northcote et al. 1978; Von Ende 1979) in which introductions of cutthroat trout (*Salmo clarki*), Dolly Varden (*Salvelinus malma*), or mudminnows (*Umbra limi*) into previously fishless lakes virtually eliminated *C. americanus* populations. Similar experiments involving *C. punctipennis* have not been performed, but liming and brook trout introduction have not significantly decreased populations of *C. punctipennis* in Woods Lake (M. Robbins, Department of Biology, Indiana University, Bloomington, IN, pers. comm.).

The hypothesis that fish predation limits the distribution of *C. americanus* but not *C. punctipennis* is also supported by observations that *C. americanus* populations do not undergo daily vertical migrations and are usually concentrated within 5 m of the water surface throughout the day (Fedorenko and Swift 1972; Pope et al. 1973; Fedorenko 1975a; Carter and Kwik 1977; Von Ende 1979), whereas *C. punctipennis* migrates vertically on a daily basis (Pope et al. 1973; Carter and Kwik 1977; Von Ende 1979). *Chaoborus americanus* populations would thus be more susceptible to fish predation than *C. punctipennis* populations, which are able to persist in lakes with fish apparently by utilizing a hypolimnetic refuge from predation. Furthermore, Von Ende (1979) demonstrated that *C. americanus* can exclude *C. punctipennis*, as well as other *Chaoborus* species, from fishless lakes by preying on their early instars. This mechanism of congeneric predation can explain the absence of *C. punctipennis* in those fishless lakes that have large populations of *C. americanus*, such as Cranberry Pond.

It is surprising, based on the information given above, that *C. punctipennis* and not *C. americanus* was present in Woods Lake prior to treatment. The absence of *C. americanus* in Woods Lake is probably the result of historical, rather than currently existing, ecological interactions. Each year from 1974 through 1977, 3000 brook trout were stocked into Woods Lake (Gloss et al. 1987). Thus Woods Lake had been without fish for no more than 6 yr when the present study began. In contrast, Cranberry Pond had been fishless for at least 23 yr (Gloss et al. 1987). This historical difference suggests that *C. americanus* was unable to colonize Woods Lake within the 6-yr period this lake was without fish.

The high population density of *C. americanus* in Cranberry Pond has probably had impacts on the species composition and life history characteristics of the crustacean zooplankton (e.g. *Diaptomus minutus*) of that lake (Schaffner 1989). In situ experiments have indicated that *C. americanus* predation can eliminate *Bosmina longirostris* from many fishless lakes (Von Ende and Dempsey 1981), and that predation by *C. abscuripes* and *Glaenocorisa propinqua* can similarly reduce the abundance of cladocerans relative to copepods (Nyman et al. 1985). Seasonal and spatial segregation and size incompatibilities have enabled several crustacean zooplanters to coexist with *C. americanus* and *C. trivittatus* (Fedorenko 1975b).

Limnetic populations of notonectids and corixids in both study lakes, and *C. americanus* in Cranberry Pond, virtually disappeared within 3 mo after treatment. These declines could result from four processes: (1) chance, (2) behavioral and within-lake distributional changes, (3) physiological stress caused by liming, and (4) direct predation by brook trout. Evidence from this and other studies suggest predation was the most important of these.

It is extremely unlikely that the virtual disappearance of these taxa in two different lakes soon after treatment was a result of chance. Even though stochastic variation in the populations of particular species and genera may occur between years, Istock (1973) found considerable stability of the aggregate population of corixids in a pond. Also, the facts that *C. americanus* recruitment took place just before and soon after treatment (Fig. 3B), and that corixid and notonectid recruitment had continued to take place in populations even as they declined (Fig. 1, 2, 4, and 5) strongly suggest that the declines were not due to chance.

Evidence indicated that Hemiptera (and Coleoptera larvae) populations decreased, rather than increased, in the benthic areas of the lakes after treatment (Table 2). It is possible, however, that populations of Hemiptera and other necktonic insects increased in shallow (< 0.5 m) littoral regions of the lakes, but no data were collected from these regions.

Physiological stress may have contributed to the declines of some of the limnetic insect populations, but was probably not as important as trout predation. The absence of larger individuals of *Dasycorixa* in Cranberry Pond and *Notonecta* in Woods Lake following treatment (Fig. 4 and 5) suggests that these early instars experienced physiological stress and/or size selective predation. Such stress could have been related to changes in water chemistry or food availability; dramatic changes in water pH (Fordham and Driscoll 1989), and declines in phytoplankton biomass (Bukaveckas 1989) and zooplankton populations (Schaffner 1989) occurred within the first month after treatment. Yet there was evidence of the growth of individuals of *Dasycorixa* in Woods Lake and *Notonecta* in Cranberry Pond during this period (Fig. 4 and 5), and no significant mortality of *C. americanus* in in situ enclosures had occurred even 61 d after liming (M. Robbins, Department of Biology, Indiana University, Bloomington, IN, pers. comm.).

Several field experiments and lake surveys have emphasized the importance of fish predation in limiting the distribution and abundance of necktonic insects in lakes and ponds. Macan (1965) concluded that brown trout (*Salmo trutta*) introductions dramatically reduced populations of *Notonecta* and certain dytiscid larvae in a moorland pond. Similarly, perch stocked into one-half of an acidified, fishless lake in Sweden eliminated the population of *Glaenocorisa propinqua* from that half of the pond (Henrikson and Oscarson 1978b). Populations of *G. propinqua* and *Chaoborus* sp. increased after the removal of fish from a small Swedish lake (Stenson et al. 1978). Populations of *G. propinqua, Cymatia bonsdorffi, Chaoborus flavicans*, and dytiscid beetles inhabiting an acidified, fishless lake in Sweden increased after it was limed but remained fishless (Henrikson and Oscarson 1984). Furthermore, Bendell and McNicole (1987) found from a survey of lakes in Canada that the presence of Corixidae, *Notonecta, Buenoa, Graphoderus liberus* (Dytiscidae), and *C. americanus* is independent of lake pH, but very strongly dependent on the presence or absence of fish. They concluded that fish predation is the most important factor limiting the distributions of these taxa. Bendell (1986) found no relationship between lake pH and population densities of *Notonecta*, but that the highest populations of *Buenoa* were in the most alkaline lakes (about pH = 8). Thus it is reasonable to speculate that corixid, notonectid, and *Chaoborus* populations in Cranberry Pond and Woods Lake would have remained near pretreatment densities, or increased as they did in the Swedish lake, if trout had not also been introduced to these lakes.

In conclusion, results of this study indicate that limnetic populations of Notonectidae, Corixidae, Dytiscidae, and certain Chaoboridae occur in acidified, fishless lakes in the Adirondack Mountains of New York. Liming and brook trout introductions to these lakes significantly reduce (or eliminate) these populations. Calculated predation by brook trout could account for most of the reductions of limnetic insect populations. Brook trout may at least temporarily derive substantial energetic benefits from these populations while they exist; *C. americanus* supplied about 50% of the energy utilized by brook trout in Cranberry Pond during the first month after treatment (Gloss et al. 1989). However, the rapid elimination of these limnetic populations documents the considerable instability of the predator–prey relationships of lakes which have been limed and had fish introduced. Consequently, initial growth rates of trout stocked into limed lakes may not be reliable indicators of equilibrium or sustainable growth rates (Nilsson 1972; Hasselrot et al. 1984; Schofield 1989).

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# Effects of Calcite Treatment on Primary Producers in Acidified Adirondack Lakes. II. Short-Term Response by Phytoplankton Communities[1]

Paul A. Bukaveckas

*Department of Biology, Indiana University, Bloomington, Indiana 47405, USA*

Bukaveckas, P. A. 1989. Effects of calcite treatment on primary producers in acidified Adirondack lakes. I. Short-term response by phytoplankton communities. Can. J. Fish. Aquat. Sci. 46: 352–359.

The effects of calcite addition on two acidic Adirondack lakes were studied by investigators participating in the Lake Acidification Mitigation Project. Changes in phytoplankton biomass, productivity, and species composition were monitored during the ice-free period prior to and following lake treatment. Changes in water chemistry following limestone addition were largely restricted to the upper water column since calcite particles applied to the lake surface did not effectively penetrate the thermocline. Increased phytoplankton production and biomass were observed during the posttreatment period. Phytoplankton densities and rates of production were similar in both the neutralized (pH > 7.5) and acidic (pH < 5.5) portions of the water column; however, species composition was markedly different. The phytoplankton assemblage of the upper water column was largely comprised of chlorophytes and chrysophytes which had not been observed prior to treatment. In contrast, the deep-water assemblage comprised many of the same taxa that had been dominant during the pretreatment period.

Des chercheurs participant à un projet sur l'acidification des lacs ont étudié les effets d'un traitement à la calcite dans deux lacs acidifiés des Adirondacks. Ils ont surveillé les changements de la biomasse, de la productivité et de la composition en espèces du phytoplancton lorsque les eaux n'étaient pas gelées, avant et après le traitement. Les changements de la chimie de l'eau qui ont suivi l'application de calcaire se limitaient dans une grande mesure à la partie supérieure de la colonne d'eau, car les particules de calcite appliquées à la surface du lac n'ont pu vraiment pénétrer la thermocline. Les chercheurs ont noté une augmentation de la production et de la biomasse phytoplanctonique après le traitement. La densité et la production du phytoplancton dans la portion neutralisée (pH sup. à 7,5) de la colonne d'eau étaient semblables à celles de la portion acide (pH inf. à 5,5); la composition en espèces était cependant nettement différente. La flore phytoplanctonique de la portion supérieure de la colonne d'eau était en grande partie constituée de chlorophytes et de chrysophytes, espèces absentes avant le traitement. En eau profonde par contre, on a retrouvé bon nombre des taxons qui dominaient déjà la faune avant le traitement.

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Atmospheric deposition of strong acids has been accompanied by changes in the chemical and biological characteristics of aquatic ecosystems in acid sensitive regions. Surveys of lakes in the northeastern United States, eastern Canada, Norway and Sweden have described consistent biotic responses to changes in lake acidity. The most conspicuous impact of chronic acidification is the decline of fish populations and their replacement by macroinvertebrates as top predators (Schofield 1976; Eriksson et al. 1980; Bendall and McNicol 1987). Reductions in species richness of zooplankton communities and the absence of large, filter-feeding herbivores such as *Daphnia* are also characteristic of acidified lakes (Nilssen 1980).

Studies on phytoplankton communities have documented altered species composition and decreased diversity associated with increasing acidity (Stokes 1986). In contrast, phytoplankton biomass and productivity have not been consistently correlated with lake acidity (Baker 1984). Studies on lakes in Sudbury (Ontario) (Kwiatkowski and Roff 1976), the Adirondacks (Hendrey 1980), and Florida (Crisman et al. 1980) report that the primary productivity of acidic lakes is lower relative to circumneutral waters in the same region. On the other hand, surveys in Norway (Raddum et al. 1980) and Sweden (Almer et al. 1978) indicate that primary productivity in acidic lakes is greater than or equal to that in circumneutral lakes.

Current understanding of the relationship between lake acidity and primary productivity is limited by a lack of data describing the mechanisms through which acidification influences higher levels of organization in aquatic ecosystems. Lake surveys provide a scale of observation suitable for documenting changes in ecosystem structure but are not designed to investigate the mechanistic processes that regulate structure or to detect changes in functional components associated with altered structure. Structural characteristics such as species composition and richness, as well as functional attributes such as primary production, can be studied by examining their response to

[1]This is part of a series of 13 papers devoted to the Lake Acidification Mitigation Project.

TABLE 1. Morphometric and chemical characteristics of study sites. pH and ANC data are for integrated water column samples collected during summer stratification. Ranges for Al and DOC based on data from C. Driscoll.

| Site Characteristics | Cranberry Pond | Woods Lake |
|---|---|---|
| Lake area ($m^2 \times 1000$) | 72 | 230 |
| Lake volume ($m^3 \times 1000$) | 207 | 802 |
| Maximum depth (m) | 7 | 12 |
| Mean depth (m) | 2.9 | 3.5 |
| Residence time (d) | 90 | 214 |
| pH | 4.7 – 4.9 | 4.9 – 5.2 |
| ANC ($\mu eq \cdot L$) | −25 – −5 | −15 – 5 |
| Monomeric Al ($\mu mol \cdot L$) | 5 – 20 | 2 – 12 |
| DOC ($\mu mol\ C \cdot L$) | 250 – 450 | 150 – 300 |

experimental manipulations of system parameters. Manipulations of lake acidity have been conducted at the Experimental Lakes Area in Ontario, Canada (Schindler et al. 1985), and in northern Wisconsin (Brezonik et al. 1986) by acidifying unimpacted lakes with direct applications of mineral acids. The Lake Acidification Mitigation Project (LAMP) is based on an alternative approach whereby the acidity of impacted Adirondack lakes is reduced by the addition of calcium carbonate. An overview of LAMP design and objectives is presented in Porcella (1989).

Research on primary producers at the LAMP study sites has focused on (1) measuring phytoplankton, periphyton, and macrophyte abundance under acidic and circumneutral conditions in order to quantify changes in primary production associated with reductions of acidity; (2) assessing community-level responses of phytoplankton and epiphytes by monitoring changes in productivity, species composition and diversity; and (3) integrating data on changes in transparency, thermal stratification, metal concentrations, nutrient availability, and zooplankton abundance in order to evaluate mechanisms through which changes in acidity influence primary production. This paper will describe short-term effects of calcite addition on phytoplankton abundance, productivity, and species composition at two LAMP study sites. Data describing spatial and temporal patterns of phytoplankton growth during the pre- and posttreatment period will be discussed in light of changes in water quality and zooplankton abundance.

## Site Description and Methods

The study sites Cranberry Pond and Woods Lake, are located in the west-central Adirondack Mountains in predominantly forested and undeveloped watersheds. Lake and watershed characteristics are summarized in Table 1. Detailed descriptions of basin morphology and watershed hydrology, geology, and vegetation are presented in Staubitz and Zarriello (1989). Pretreatment water chemistry data are described in Fordham and Driscoll (1989) and Driscoll et al. (1989a, 1989b) and will be briefly summarized. Chemical characteristics of both sites were similar and typical of clearwater acidic lakes in the Adirondack region (see Table 1). Sulphate was the dominant anion and the equivalence of acidic anions exceeded base cations, resulting in pH values less than 5, negative acid neutralizing capacity and generally high concentrations of aluminum, predominantly as the labile (monomeric) fraction.

Phytoplankton samples were collected over the deepest portion of the lake basin at 5- to 10-d intervals during the ice-free period. Small diameter tubing was lowered to within one meter of the lake bottom to obtain integrated water column samples. Discrete depth samples were collected at 1- to 2-m intervals from the surface to the bottom. Samples were preserved in the field and retained for phytoplankton identification and enumeration or stored in the dark for subsequent analyses of photosynthetic pigments.

Phytoplankton samples were preserved by the addition of 50:50 glutaraldehyde–formaldehyde to a final concentration of 3% preservative. Samples were processed using a modification of the permanent slide mounting technique developed by Dozier and Richerson (1975). Slide mounts were prepared by drawing measured volumes of sample through syringe-mounted millipore HA filters (0.45 μm) and clearing in glutaraldehyde. Phytoplankton were examined under a magnification of 1250 × using enhanced contrast optics. Two to four replicate slides were prepared from each phytoplankton sample and counted at 500 ×. Error associated with calculated cell concentrations was estimated from the variance between replicate slide counts.

Samples for pigment analyses were processed within 1–2 h of collection by filtration through Gelman A/E glass fiber filters and extraction in aqueous (90%) acetone. Filters were macerated using a Teflon tissue grinder and steeped for 12 h in the dark at 4°C. Extracts were analyzed using a Varian DMS 70 spectrophotometer equipped with long path length (4 cm) cells and narrow (1 nm) bandwidth. Chlorophylls *a*, *b*, and *c* were determined from optical density readings at 663, 645, and 630 nm using the trichromatic equations of Jeffrey and Humphrey (1975). Concentrations of chlorophyll degradation products were determined by measuring the optical density of the extract before and after acidification with 0.1 M HCl. Estimates of chlorophyll *a* corrected for phaeophytin *a* were calculated using the Lorenzen equations as modified by Speziale et al. (1984).

Phytoplankton productivity was measured at 10- to 20-d intervals by the $^{14}C$ isotope technique described by Vollenweider (1969). Samples were collected using a nonmetallic Kemmerer sampler and incubated in 300-mL light and dark BOD bottles. Each bottle was injected with 5 μCi radiocarbon as sodium bicarbonate. Two light and two dark bottles were incubated at each of three depths (Cranberry Pond: 2, 4, and 6 m, Woods Lake: 3, 7, and 11 m) for 4 h at midday (1000–1400). Samples were placed on ice and kept dark during transport to the laboratory (< 1 h). Labelled phytoplankton were collected on millipore HA membrane filters (0.45 μm) under low vacuum pressure. Filters were rinsed with acidified water and placed in scintillation vials containing 0.1 mL of 1 M HCl to remove unincorporated isotope (Lean and Burnison 1979). After 2–3 h fluor was added (Aquasol-2, New England and Nuclear Products) and activity was measured on a Beckman LS-233 liquid scintillation counter. Quenching was corrected by the external standard channels ratio technique. Concentrations of dissolved inorganic carbon were measured by gas chromatography as part of the water chemistry sampling program at the LAMP study sites (Fordham and Driscoll 1989).

## Results

### Pretreatment Characterization

The phytoplankton floras of Cranberry Pond and Woods Lake were similar and characteristic of acidic lakes in Sweden (Almer et al. 1978), the Adirondacks (Hendrey 1980; Charles 1982), and the Sudbury region of Ontario (Kwiatkowski and Roff

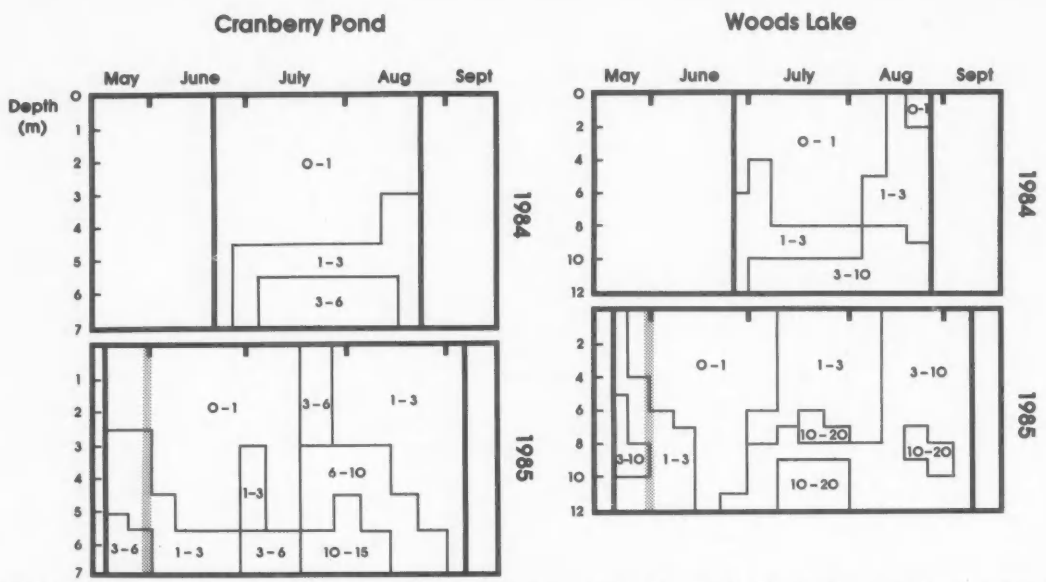


FIG. 1. Pre- and posttreatment chlorophyll isopleths (micrograms per litre corrected for phaeophytin) for Cranberry Pond and Woods Lake.

1976, Yan 1979). Dominant phytoplankton genera included the chrysophytes *Dinobryon* and *Mallomonas*, the cryptophyte *Cryptomonas* and the dinoflagellates *Peridinium* and *Gymnodinium*. These taxa accounted for over 80% of the total cell density. Other taxa commonly encountered included a number of chlorophytes (*Kirchneriella, Scenedesmus, Schroderia*, and unidentified coccoids) and several species of *Merismopedia*. Pennate diatoms were consistently observed in water column samples, although estimated densities were extremely low. *Navicula tenuicephala, Anomoeoneis serians*, and *Tabellaria flocculosa* were the most abundant diatoms and annually accounted for over 90% of the individuals in this category. Since these taxa are abundant in epiphyton samples collected from these sites (P. Bukaveckas, unpubl. data), their occurrence in the water column may be a result of detachment and transport from the littoral zone.

Patterns of phytoplankton seasonal succession and vertical distribution were similar at both sites. During early- and mid-summer, cell densities within the epilimnion were extremely low, corresponding to chlorophyll concentrations of less than 1 $\mu g \cdot L^{-1}$ (Fig. 1) and carbon uptake rates less than 1 mg $C \cdot m^{-3} \cdot h^{-1}$. Highest estimates of phytoplankton abundance and productivity were associated with deep-water chlorophyll maxima. Carbon uptake rates measured at the chlorophyll peak were consistently greater than rates measured in the upper water column. The chlorophyll maxima typically occurred within 1–2 m of the sediment-water interface and its position did not vary in response to seasonal changes in thermocline depth. Although both sites exhibited only weak thermal stratification during late summer, the deep-water chlorophyll peak persisted throughout the sampling period.

During early summer, the deep-water assemblage was dominated by chrysophytes, particularly *Dinobryon bavaricum* and several species of *Mallomonas*. During mid-summer, *Cryptomonas* spp. and *Peridinium inconspicuum* were the most abundant taxa in samples collected from the chlorophyll maxima although both were poorly represented in the epilimnion. Phytoplankton biomass increased throughout the water column in late summer owing to higher densities of small chlorophytes, particularly *Kirchneriella obesa* and small (<10 μm) coccoid unicells.

Treatment Effects.

An account of the chemical response following limestone addition is presented in Fordham and Driscoll (1989) and Driscoll et al. (1989a, 1989b) and will be summarized briefly. On 30 and 31 May 1985, a high purity calcite slurry (98% calcium carbonate containing 71% solids by weight) was applied by helicopter to Cranberry Pond (10 t) and Woods Lake (32 t). Owing to the onset of thermal stratification prior to the treatment period, the calcite particles (median diameter 2 μm) did not effectively penetrate the thermocline. As a result, changes in water chemistry were limited to the mixed depth of Cranberry Pond (5 m) and Woods Lake (8 m). At Woods Lake, marked increases in epilimnetic pH (from 4.9 to 9.4), acid neutralizing capacity (from 11 to 218 $\mu eq \cdot L^{-1}$ and dissolved inorganic carbon (from 41 to 202 $\mu mol\ C \cdot L^{-1}$) were measured immediately (24 h) after application of the calcite slurry. Within the hypolimnion of Woods Lake, pH values remained below 6 and ANC remained less than 100 $\mu eq \cdot L^{-1}$ throughout the summer period. Similar trends were evident in Cranberry Pond, but owing to its weaker stratification, greater transport of calcite particles was observed through the metalimnion. A shift in the speciation of aluminum from acid-soluble to monomeric forms was observed at both sites (Driscoll et al. 1989b). Within 6–8 wk following treatment, monomeric aluminum concentrations were reduced by an order of magnitude.

At both sites, chlorophyll concentrations were reduced following base application (Fig. 2). Epilimnetic chlorophyll decreased by 50% within 3–4 d following treatment and after 10–11 d declined to less than 25% of pretreatment levels. Chlorophyll measured at the deep-water maxima declined over a period of 17–18 d to levels matching those observed in the

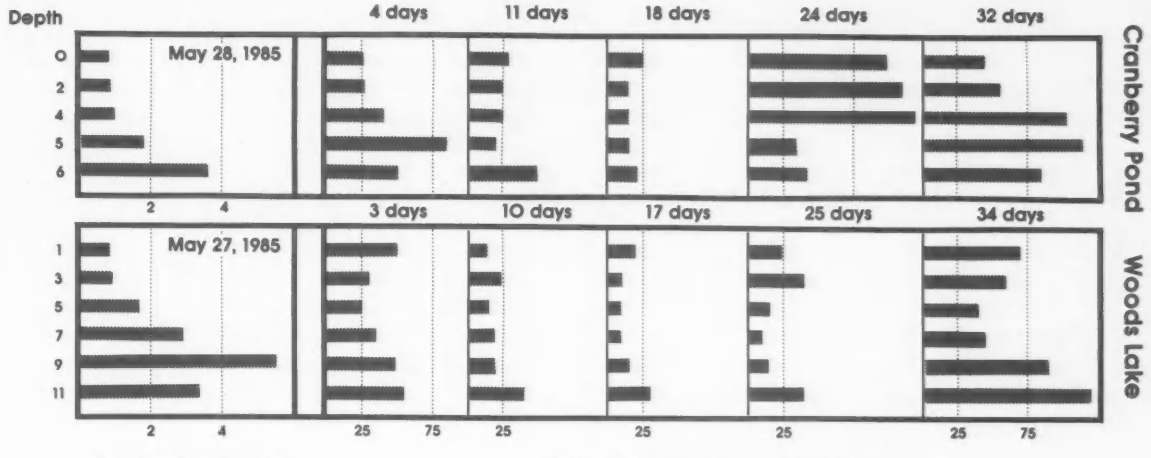


FIG. 2. Posttreatment chlorophyll profiles (as percent of pretreatment concentrations) for Cranberry Pond and Woods Lake.

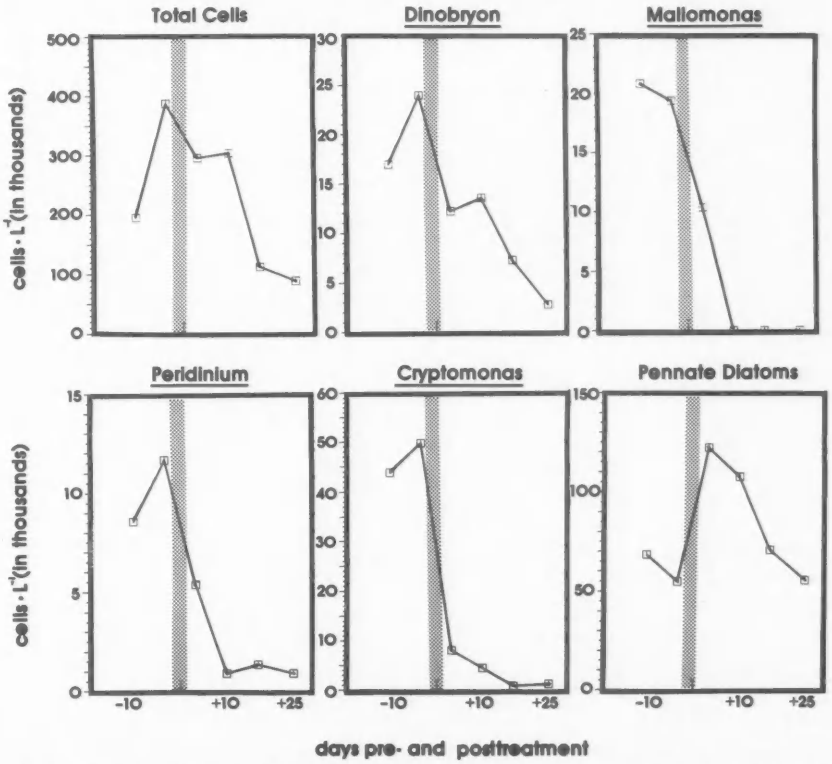


FIG. 3. Posttreatment phytoplankton densities (as cells per litre) from integrated water column samples collected at Woods Lake.

mixed zone. Rates of carbon uptake during the period of reduced pigment levels were less than 0.5 mg $C \cdot m^{-3} \cdot h^{-1}$ at all depths and were only slightly greater than dark bottle values and zero time blanks.

Corresponding to changes in chlorophyll, significant reductions in phytoplankton density were observed following base addition (Fig. 3). Changes in phytoplankton community composition were marked by the decline of dominant taxa including *Cryptomonas*, *Mallomonas*, *Peridinium*, and *Gymnodinium*. At Woods Lake, loricas of *Dinobryon bavaricum* and *D. acuminatum* remained in suspension below the thermocline for 10 d after treatment but contained cells in poor condition which were probably senescent. Pennate diatoms were the only taxa to exhibit an increase in abundance following calcite addition. Many of the diatoms encountered during this period had not been previously observed in plankton samples but were com-

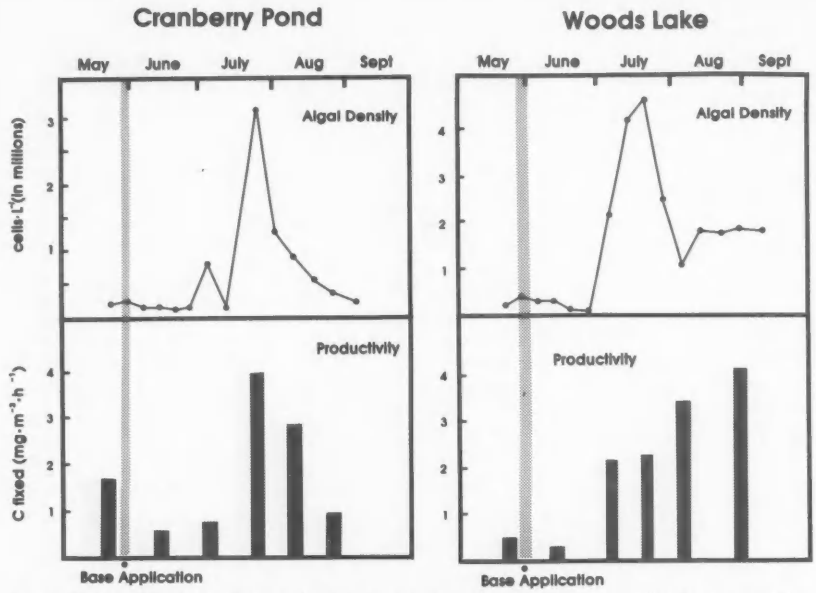


FIG. 4. Phytoplankton abundance estimated from integrated water column samples (as cells per litre, in millions) and productivity (milligrams of carbon per metre cubed per hour) calculated as a water column average prior to and following treatment of (a) Woods Lake and (b) Cranberry Pond.

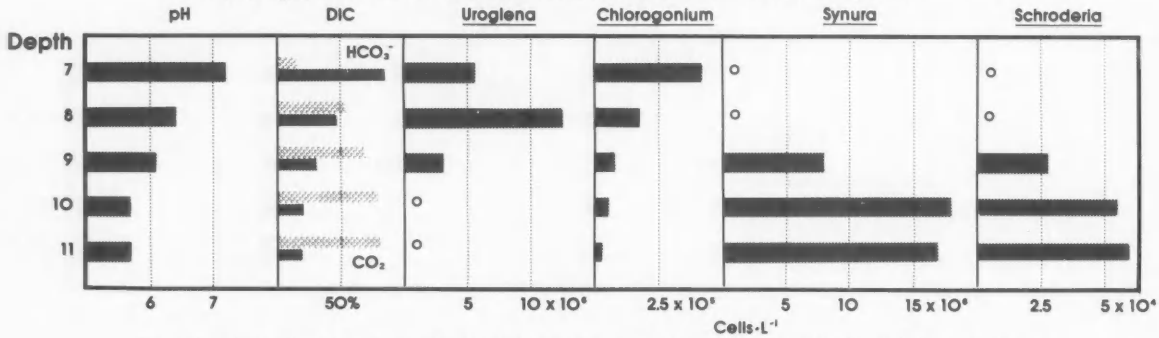


FIG. 5. Depth profiles of dominant phytoplankton taxa from Woods Lake in relation to pH and DIC speciation.

mon in the epiphytic community (P. Bukaveckas, unpubl. data). Their occurrence in the water column coincided with the dieback of the dominant macrophyte in Cranberry Pond and Woods Lake (*Utricularia purpurea*; Bukaveckas 1988). Chloroplast structure of the diatom cells was poor, suggesting that their presence in the plankton was due to detachment from decaying plants rather than active growth in the water column.

Increasing chlorophyll concentrations were initially observed 24 d after treatment in the upper water column of Cranberry Pond (Fig. 2). At both sites, chlorophyll levels below the thermocline began to increase 32–34 d posttreatment. Chlorophyll continued to increase in the upper and lower water column until maximum levels were reached during mid-July, approximately 50 d after limestone addition (Fig. 1). During the period of maximal standing crop, phytoplankton densities in integrated samples exceeded 4 million cells·$L^{-1}$ at Woods Lake and 3 million cells·$L^{-1}$ at Cranberry Pond (Fig. 4). In comparison, estimates during July of the previous year were less than 0.5 million cells·$L^{-1}$ at both sites. Corresponding to greater phytoplankton abundance, productivity increased in the upper and lower water column at both sites. Rates of carbon uptake at the depth of the chlorophyll maxima ranged from 4 to 6 mg C·$m^{-3}$·$h^{-1}$ compared with less than 1 mg C·$m^{-3}$·$h^{-1}$ measured during the pretreatment period.

During the period of maximal standing crop, vertical patterns of phytoplankton distribution were atypical in that two distinct chlorophyll peaks were observed in the water column of Woods Lake (Fig. 1). The upper peak occurred above the thermocline in the neutralized (pH $> 7.5$) portion of the water column. A second peak developed below the thermocline in the acidic (pH $< 5.5$) hypolimnion. Phytoplankton densities and rates of production were similar in both the upper and lower chlorophyll peaks, however, species composition was markedly different (Fig. 5). The epilimnetic phytoplankton assemblage was dominated by a chlorophyte, *Chlorogonium*, and a colonial chrysophyte *Uroglena*. These taxa had not been previously observed in plankton samples collected at these sites. In contrast, the deep-water assemblage was comprised of many of the same taxa which were present prior to treatment. The chlorophyte *Schroderia* and a colonial chrysophyte *Synura* dominated the hypolimnetic phytoplankton community.

TABLE 2. Dominant taxa comprising the pre- and posttreatment phytoplankton assemblage categorized on the basis of their response to treatment and their occurrence in the upper (neutralized) or lower (acidic) water column.

| | | |
|---|---|---|
| Group 1. Taxa occurring before but not after treatment. | | |
| *Peridinium* | (Dinoflagellate) | |
| *Gymnodinium* | (Dinoflagellate) | |
| *Mallomonas* | (Chrysophyte) | |
| Group 2. Taxa occurring after but not before treatment. | | |
| Uroglena | (Chrysophyte) | upper only |
| Chlorogonium | (Chlorophyte) | upper only |
| Aphanothece | (Cyanophyte) | upper only |
| Synedra | (Diatom) | upper only |
| Elakatothrix | (Chlorophyte) | upper only |
| Group 3. Taxa occurring both before and after treatment. | | |
| *Cryptomonas* | (Cryptophyte) | lower only |
| *Schroderia* | (Chlorophyte) | lower only |
| *Gloeothece* | (Cyanophyte) | lower only |
| *Synura* | (Chrysophyte) | lower only |
| *Dinobryon* | (Chrysophyte) | upper and lower |

TABLE 3. Estimates of Secchi depth and coefficients of light attenuation and scattering measured prior to and following base addition to Woods Lake on May 30–31.

| | May 20 | May 27 | June 3 | June 10 | June 17 |
|---|---|---|---|---|---|
| Secchi Depth (m) | 5.7 | 5.4 | 0.6 | 4.8 | 7.9 |
| Attenuation | 0.51 | 0.34 | 0.76 | 0.52 | 0.39 |
| Scattering | 0.25 | 0.17 | 5.68 | 1.82 | 0.16 |

During late-July phytoplankton densities decreased due to the decline of colonial chlorophyte and chrysophyte populations in the upper and lower water column. Silicious cysts were frequently observed in samples collected during the period of senescence. Dominant taxa comprising the late summer metalimnetic population included *Dinobryon bavaricum, Elakatothrix gelatinosa, Synedra* sp. (PIRLA No. 9; Camburn et al. 1986) and small (<10 μm) coccoid unicells. Highest densities of these taxa occurred above the thermocline, but as the water column approached isothermal conditions, the depth of the maxima descended into the deeper (acidic) region.

In Cranberry Pond, changes in species composition during the posttreatment period were similar to those observed at Woods Lake. Differences in species composition between the neutralized and acidic portions of the water column were less dramatic but exhibited the same trends. Patterns of phytoplankton growth and abundance were similar at both sites during early and mid-summer. During August, chlorophyll concentrations, phytoplankton densities, and productivity in Cranberry Pond declined to pretreatment levels (Fig. 1 and 4). In Woods Lake, productivity continued to increase during late summer despite reductions in phytoplankton density. Phytoplankton abundance and productivity remained significantly higher relative to the pretreatment period throughout the sampling period at Woods Lake.

Phytoplankton taxa occurring in Cranberry Pond and Woods Lake were categorized based on their response to treatment (Table 2). Group 1 comprised taxa which were present before but not after treatment. Group 2 comprised taxa which were present after but not before treatment. Group 3 comprised taxa which were observed both before and after treatment. Taxa comprising the posttreatment assemblage (Groups 2 and 3) were further categorized based on their occurrence in the upper (treated) or lower (acidic) water column. Of the taxa which had been dominant before treatment, only the dinoflagellates (*P. inconspicuum* and *Gymnodinium* sp.) and *Mallomonas* were not observed during the posttreatment period. All other taxa present during the pretreatment period exhibited increased abundance following base addition (Group 3). Of these, all but *Dinobryon bavaricum* were restricted in their vertical distribution to the acidic portion of the water column. In contrast, taxa which were present after but not before treatment were restricted to the upper water column (Group 2).

## Discussion

Decreased densities of phytoplankton and zooplankton following base application have been reported previously (Scheider et al. 1975; Hultberg and Andersson 1982); however, the mechanisms responsible for the observed effects are not completely understood. Reductions in biomass may be attributed to mortality induced by rapid chemical changes, or may be a result of physical removal by coagulation with hydrolyzing metals or be cell adsorption onto sinking mineral particles (Baker et al. 1984). Sedimentation of phytoplankton from the upper water column and subsequent lysis of cellular contents may have contributed to the increase in DOC observed above the thermocline of Woods Lake several days following treatment (see figure 3, Driscoll et al. 1989b). These mechanisms, however, do not account for reduced phytoplankton densities measured below the maximum depth of particulate penetration in Cranberry Pond and Woods Lake. Decreased phytoplankton growth below the thermocline may be attributed to reduced irradiance, since light penetration following calcite addition was severely attenuated by scattering within the epilimnetic layer (Table 3). Light levels corresponding to the depth of the chlorophyll maxima decreased to less than 1% of subsurface irradiance at both sites immediately after base application. By comparison, irradiance at the chlorophyll maxima before treatment ranged from 10 to 25% of subsurface measurements at Cranberry Pond and 5 – 10% of subsurface values in Woods Lake. Changes in light climate attributable to scattering persisted for fewer than 10 d at both sites due to the rapid dissolution of the small mineral particles. Therefore, although changes in light climate may contribute to the decline of the deep-water assemblage, they do not account for the prolonged (24–25 d) suppression of phytoplankton growth observed throughout the water column at both sites.

The period during which phytoplankton growth was suppressed corresponds to the period when the partial pressure of $CO_2$ was highly undersaturated with respect to atmospheric equilibrium. Althugh the concentration of dissolved $CO_2$ in an air equilibrated solution does not vary as a function of pH, the rate of calcite dissolution exceeded the rate of influx of atmospheric $CO_2$ and, as a result, $CO_2$ was severely depleted within the epilimnion of both Cranberry Pond and Woods Lake (see figure 1e in Fordham and Driscoll 1989). It is likely that the pretreatment phytoplankton assemblage was dependent upon $CO_2$ as an inorganic carbon source for photosynthesis, since under acidic conditions (pH below 5) it is the predominant form of DIC. Following calcite addition phytoplankton growth may have been carbon limited due to the depletion of dissolved $CO_2$ despite elevated concentrations of carbonate forms of DIC. If the hypothesis that $CO_2$ availability limited phytoplankton

growth was correct, reductions in biomass would be predicted to persist until (1) rates of calcite dissolution diminished, allowing equilibration with atmospheric $CO_2$ to occur, (2) phytoplankton adapted to growth under acidic conditions ($CO_2$ utilization) were able to initiate biochemical pathways enhancing uptake of $HCO_3^-$, or (3) new phytoplankton taxa adapted to using $HCO_3^-$ for photosynthesis replaced the pretreatment assemblage. The influence of physico–chemical (calcite dissolution), biochemical (carbon utilization), and community-level (species replacement) constraints on posttreatment phytoplankton growth will be considered.

Increasing chlorophyll concentrations were initially observed near the surface, where equilibration of $CO_2$ would be expected to occur most rapidly. Higher growth rates were observed at Cranberry Pond which, owing to its greater surface area to volume ratio, equilibrated more rapidly than Woods Lake (Fordham and Driscoll 1989). Following the period of equilibration, chlorophyll concentrations and phytoplankton densities increased at a faster rate in the lower water column compared with the epilimnion. In the acidic hypolimnion, DIC was predominantly in the form of dissolved $CO_2$ and the phytoplankton assemblage was comprised of the same taxa which had been present prior to treatment (Group 2). As a result, growth rates would not be temporally constrained by physiological (adaptation to $HCO_3^-$ utilization) or community level (species replacement) responses. In the epilimnion, increased phytoplankton abundance coincided with the replacement of the pretreatment assemblage by taxa presumably more capable of fixing bicarbonate forms of DIC for photosynthesis (Group 3).

Taxa which occurred in the upper water column were rare or absent in the hypolimnion. Furthermore, with the exception of *D. bavaricum*, taxa comprising the pretreatment community were unable to persist in the upper (neutralized) portion of the water column. These observations suggest that species adapted to growing under acidic or circumneutral conditions may be limited in their capacity to alter patterns of DIC utilization. Therefore, changes in the carbon equilibrium may play an important role in determining the species composition of phytoplankton communities in acidified or neutralized lakes. The importance of DIC speciation in influencing the species composition of aquatic macrophyte communities has also been suggested (Wetzel et al. 1985; Francko 1986; Bukaveckas 1988).

Alternatively, patterns of phytoplankton zonation and species succession may be accounted for by changes in DIC concentration rather than speciation. Laboratory experiments have demonstrated that the levels of DIC which occur in acidic lakes are below the photosynthetic compensation point of some species (Williams and Turpin 1987). If inorganic carbon is an important rate-limiting resource at low pH, then changes in phytoplankton species composition following base addition may reflect increased DIC availability rather than changes in the carbon equilibrium. Species with higher DIC affinities would continue to dominate the lower water column but could be excluded from the upper water column if species comprising the epilimnetic assemblage were superior competitors for other nutrients. The relative importance of changes in the carbon equilibrium and DIC concentration can not be assessed from the field data since the patterns of phytoplankton zonation follow both a pH and DIC gradient.

Although changes in DIC concentration and speciation may be important in influencing shifts in species composition, it is unlikely that these mechanisms are important in regulating changes in total biomass following the period of $CO_2$ equilibration. Vertical patterns of biomass distribution did not correspond to water column DIC gradients. Both the epilimnetic and hypolimnetic assemblages displayed the same treatment response despite experiencing significantly different environments with respect to pH and DIC. Corresponding changes of productivity and biomass in the upper and lower portions of the water column suggest that the effect of base application on mechanisms influencing growth rates and loss rates was not restricted to the mixed zone. Posttreatment increases in phytoplankton abundance may reflect increased nutrient availability following the removal of phosphorus complexing agents such as aluminum from the water column. Concentrations of labile (monomeric) aluminum were reduced from 10 to less than 3 $\mu mol \cdot L^{-1}$ within 6 – 8 wk after treatment (see figure 7, Driscoll et al. 1989b). Greater nutrient availability may also be attributed to low uptake rates during the period preceeding $CO_2$ equilibration. The decline of phytoplankton populations and the dieback of extensive macrophyte beds (*Utricularia purpurea*) would also result in reduced rates of nutrient removal. Furthermore, decomposition of macrophyte biomass would increase in-lake generation of nitrogen and phosphorus.

Increasing phytoplankton growth rates may have been accompanied by reduced loss rates following the decline of zooplankton populations. Dominant zooplankton taxa exhibited 90% mortality within 1 wk after treatment (Schaffner 1989). During late August, reductions in phytoplankton abundance corresponded to the recovery of the zooplankton assemblage and to the appearance of *Daphnia catawba*. In Cranberry Pond, *D. catawba* appeared earlier and was more abundant than in Woods Lake. Grazing by this species may have contributed to the more rapid decline in phytoplankton density observed at this site. In Woods Lake, the increase in grazer abundance during late summer corresponded to an increase in productivity per unit of biomass and an increase in the abundance of small coccoid unicells.

In summary, changes in the concentration and speciation of inorganic carbon may play an important role in determining the species composition of acidified and neutralized lakes. However, other factors, such as nutrient availability and zooplankton grazing pressure, may be more important in regulating phytoplankton abundance. Calcium carbonate application may alter the nutrient status of acidified lakes by removing monomeric aluminum from the water column. Additional data will be required to assess the relative importance of changes in zooplankton grazing pressure and changes in nutrient availability in regulating phytoplankton abundance in acidified and neutralized lakes.

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# REVIEWS/SYNTHÈSES

# Organochlorines and Marine Mammal Reproduction

R. F. Addison

*Physical and Chemical Sciences, Department of Fisheries and Oceans, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S. B2Y 4A2*

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Reproductive failures in four populations of marine mammals (Californian sea lions (*Zalophus californianus*), Bothnian Bay ringed seals (*Pusa hispida*), Dutch Waddensee harbour seals (*Phoca vitulina*), and most recently, Gulf of St. Lawrence beluga whales (*Delphinapterus leucas*)) have been attributed to the effects of contamination by organochlorine (OC) residues. In this article, I review the evidence for these effects. I conclude that since (a) crucial biological information in the light of which OC residue data can be interpreted is often missing, (b) the nature of the supposed reproductive effect is variable, and (c) the OC residues to which these effects are attributed vary qualitatively and quantitatively, correlations between observed residue concentrations and apparent reproductive changes do not provide any firm evidence for a cause – effect relationship. In a single experimental study, a diet with a higher OC content than that used as a control impaifed reproduction in harbour seals; however, dietary components other than OC content also differed. Although there appears to be no firm correlative evidence linking residue concentrations in marine mammals with reproductive effects, there is enough concern about possible links to justify more experimental studies, with the aim of identifying the possible biochemical mechanisms involved.

La baisse de la reproduction dans quatre populations de mammifères marins (lion de mer de la Californie (*Zalophus californianus*), phoque annelé du golfe de Botnie (*Pusa hispida*), phoque commun de la Waddenzee hollandaise (*Phoca vitulina*), et, plus récemment, béluga du golfe du Saint-Laurent (*Delphinapterus leucas*)) a été attribuée aux contaminants organochlorés (OC). Dans cet article, nous examinons les données rassemblées sur la gestion. Nous concluons que les corrélations reliant les concentrations mesurées et les changements apparents de la fonction reproductive n'apportent aucune preuve formelle de l'existence d'une relation de cause à effet étant donné qu'il manque dans bien des cas d'importants renseignements d'ordre biologique pour l'interprétation des données concernant les résidus d'OC, que l'effet qu'on présume s'exercer sur la reproduction est variable et que les caractéristiques qualitatives et quantitatives des résidus d'OC auxquels on attribue cet effet sont variables. Dans une seule étude expérimentale, on a noté que la reproduction est perturbée chez des phoques communs dont la nourriture contenait une plus grande proportion d'OC que celle des sujets témoin; toutefois, d'autres composants alimentaires différaient également. Il semble qu'aucune corrélation ne prouve formellement l'existence de liens entre la concentration de résidus dans les tissus des mammifères marins et des effets quelconques sur la reproduction, mais l'éventualité qu'une telle relation existe suscite assez d'inquiétude pour qu'il soit justifié d'entreprendre d'autres études expérimentales afin de déterminer quels mécanismes biochimiques pourraient être mis en jeu.

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Marine mammals usually occupy high trophic levels in marine food webs, and so may accumulate large body burdens of organochlorine (OC) pollutants, such as the DDT group of insecticides and the polychlorinated biphenyls (PCBs). During the last 20 yr or so, reproductive disorders in four marine mammal populations have been attributed to high tissue OC concentrations in the affected animals. Evidence for such effects comes mostly from correlations between the reproductive changes observed and tissue OC concentrations, rather than from experimental proof of a cause – effect relationship. In this paper, I review the published evidence linking OC concentrations with reproductive changes in marine mammals. Since the literature covers a long period during which sampling and analytical approaches have evolved, some introductory comments on methods may be helpful.

## Methods

In the early 1970s most OC analyses involved residue separation by packed column gas – liquid chromatography (GLC), followed by estimation in an electron capture detector (ECD). The "clean-up" methods did not allow much fractionation within the OC groups, particularly in the isolation of PCBs from other OCs. Initial identifications and estimations were usually confirmed by chemical modification of the residues (e.g. by dehydrochlorination: Holden and Marsden 1967; or oxidation: Miles 1972) followed by rechromatography. Occasionally thin layer chromatography (TLC) was used as a confirmatory procedure.

During the 1970's, analytical methods improved. "Clean-up" approaches changed only slightly, but the introduction of

capillary column GLC with ECD made isolating and estimating OCs simpler and more informative. Separations are now so good and identification by retention time measurement is so reliable that confirmatory methods are used less than previously, and gas-chromatography – mass-spectrometry (GC–MS) is now available in many laboratories for structure identification. Thus, analyses may now be more reliable and detailed than those made 15 or 20 yr ago, and this must be considered when assessing the older literature. This is illustrated by the measurement of PCBs; the PCB concentration in an environmental sample measured by comparing the major peaks of the Aroclor 1254 "envelope" from packed column GLC (as was the practice a decade or so ago) is about four times higher than that obtained by summing the individual congeners isolated by capillary column GLC. This is because the PCB congener distribution in environmental samples is simpler than that in commercial mixtures such as Aroclor 1254, and therefore less representative of the total "envelope."

Concentrations of OC residues in marine mammal tissues vary with physiological factors, and these also must be considered in assessing residue data. The most important are age, sex, and condition. Blubber OC concentrations (the tissues most often analysed) generally increase with age in male seals and in some other marine mammals like walruses but not in females (Addison et al. 1973; Addison and Smith 1974; Helle et al. 1976b; Donkin et al. 1981; Born et al. 1981). There is a negligible increase with age in females because they mobilize and excrete large amounts of lipid and its associated residue burden during lactation (Addison and Brodie 1977; 1987). Residue concentrations in blubber are usually inversely related to condition; as fat is metabolised for energy production, the remaining OCs become more concentrated, or as fat is laid down during feeding, the existing OCs become diluted. Thus, OC residue concentrations in blubber are inversely related to blubber thickness (Addison and Smith 1974; Drescher et al. 1977; Donkin et al. 1981; Van der Zande and De Ruiter 1983).

One final aspect of sampling which should be considered is that of residue distribution around the animal. In one study (Addison et al. 1973) we found no difference in OC concentration in blubber sampled from four points in a harp seal (*Pagophilus groenlandicus*), nor was there any stratification among layers of blubber. Tanabe et al. (1981) found no variation in blubber OC concentrations at different points on the body of the striped dolphin (*Stenella coeruloalba*). However, there is no other information about this subject. Usually, only a tiny fraction of the available blubber is analyzed, and this may not be representative of the total, especially in larger mammals like whales.

In summary, to interpret blubber OC residue concentrations, we need to know the analytical methods used in their measurement, and the age, sex, and condition of the specimens analysed. Although information about analytical procedures is usually available, relevent biological information is often missing.

## Case Histories: California Sea Lions in the Early 1970s

Le Boeuf and Bonnell (1971) reported that California sea lions (*Zalopus californianus*) contained "extraordinary" concentrations of the DDT group of insecticides. The animals (one female and 24 males) had been sampled in the fall of 1970 between San Francisco and Los Angeles, and had been grouped into "healthy" animals, those found "sick" (subsequently attributed to infection by *Leptospira*, a bacteria-like organism which causes swine to abort: Smith et al. 1974a) and some found stranded, dead (presumably also infected by *Leptospira*). The methods used would not have separated PCBs so the concentrations of DDT-group residues reported (over 1000 $\mu g \cdot g^{-1}$ wet weight in blubber; Table 1) might be overestimated. There was no obvious or significant difference in residue levels between healthy, sick, and dead groups; there was a steady decline in (my) calculated mean lipid content over that series, but the statistical significance of this cannot be assessed.

Le Boeuf and Bonnell (1971) implied that the high OC concentrations in these sea lions might be associated with reproductive changes. The connection was proposed explicitly by DeLong et al. (1973) who analysed sea lions sampled from the same area in the spring of 1970. Females reproducing at full term contained much lower OC concentrations (mainly of the DDT-group and the PCBs) than those giving birth prematurely; blubber wet weight concentrations of PCB and the DDT-group in normal animals were 17 and 100 $\mu g \cdot g^{-1}$ and in the "premature" group were 100 and 800 $\mu g \cdot g^{-1}$, respectively (Table 1). Blubber lipid contents did not differ significantly between the two groups, but maternal liver and pup brain contained lower lipid (and therefore higher PCB and DDT-group concentrations on a lipid weight basis) in the premature than in the full-term group. No *Leptospira* infection was observed in the premature group.

Buhler et al. (1975) also analysed OC residues in this population; they sampled male animals which migrated northward off Oregon in 1970, 1971, and 1973. Blubber DDT-group concentrations were around several hundred $\mu g \cdot g^{-1}$ (wet weight) and PCBs about one-tenth of that. No other residues were detected. Concentrations of the DDT group and PCBs in muscle, liver, and brain were also reported. There was no consistent difference between healthy and *Leptospira*-infected animals, liver *p,p'*-DDE being higher in the latter but liver PCB lower.

Gilmartin et al. (1976) tried to separate the possible influences of high OC concentrations and *Leptospira* infection on premature births in a sea lion sample taken in 1972. Again, females bearing pups prematurely were younger and had higher concentrations of both the DDT-group and the PCBs than had full-term animals. However, the distribution of *Leptospira* between the two groups was less distinct; four out of 10 "premature" adults showed a serologic response to *L. pomona* antibodies, as did one (or two) out of 10 of the full-term females. (There seems to be some inconsistency in the data; table 2 of Gilmartin et al. (1976) shows two full-term adults with positive *Leptospira* responses, whereas the text, and that of Smith et al. (1974b) discussing the same data set, describe only one of the full-term group as having the infection.) Also, all 20 females showed a response to serotypes of the San Miguel Sea lion Virus (SMSV). This had been previously shown to be serologically identical to Vesicular Exanthema of Swine Virus (VESV) which causes abortions in swine (Smith et al. 1974a).

Most analyses of these animals refer to residue concentrations in blubber, but other tissues have been examined, though less systematically. However, analyses of brain, liver, and kidney do not as a rule shed much light on the variability in the blubber residue concentrations. In general, residue concentrations in these tissues follow similar trends to those in blubber; in some cases, low tissue lipid levels are associated with higher residue concentrations on a lipid weight (though not necessarily on a fresh weight) basis; c.f. premature versus full-term pups (Table 2).

TABLE 1. OC residues in Californian Sea Lion blubber ($\mu g \cdot g^{-1}$ wet weight, mean ± SD. NA = not analysed, ND = not detected, NR = not reported, SMSV = San Miguel Sea Lion Virus (see text), Calc. = author's recalculated data.

| Sample type | Site | Date | Number, sex | % Lipid | $p,p'-$DDE | Σ DDT | PCB | *Leptospira* present | SMSV present | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Healthy | Southern California | Fall 1970 | 4, M 1, F | 74.3 (Calc.) | 852 (Calc.) | 906 ±640 | NA | NR | NR | Le Boeuf and Bonnell 1971 |
| Sick, killed | Southern California | Fall 1970 | 6, M | 67.4 (Calc.) | 648 (Calc.) | 689 ±164 | NA | NR | NR | Le Boeuf and Bonnell 1971 |
| Dead, stranded | Southern California | Fall 1970 | 14, M | 59.6 (Calc.) | 945 (Calc.) | 1006 ±645 | NA | NR | NR | Le Boeuf and Bonnell 1971 |
| Full-term 12 yr | Southern California | Spring 1970 | 4,F | 85 | 80–93% Σ DDT | 103 ±70 | 17 ±6.1 | NR | NR | DeLong et al. 1973 |
| Premature 8 yr | Southern California | Spring 1970 | 6,F | 84 | 80–93% Σ DDT | 824 ±168 | 112 ±24 | ND | NR | DeLong et al. 1973 |
| Full-term 12 yr | Southern California | Spring 1972 | 10,F | NR | 83 ±102 | 88 ±105 | 13.2 ±11.6 | 1 (or 2?) /10 | All | Gilmartin et al. 1976 |
| Premature 8 yr | Southern California | Spring 1972 | 10,F | NR | 630 ±258 ($n$ = 8) (Calc.) | 652 ±254 ($n$ = 8) (Calc.) | 57 ±17 ($n$ = 8) (Calc.) | 4/10 | All | Gilmartin et al. 1976 |
| Healthy 4–8 yr | Oregon | Fall 1971 | 6,M | 41.6 ±25.3 | 253 ±116 | 272 (Calc.) | 34 ±21 | NR | NR | Buhler et al. 1975 |
| Healthy 4–6 yr | Oregon | Fall 1973 | 3,M | 64.7 ±6.8 | 342 ±234 | NR | 21 ±2 | NR | NR | Buhler et al. 1975 |
| Sick | Oregon | Fall 1970 | 7,M | 56.4 ±10.6 | 358 ±213 | NR | 24.2 ±11.5 | Inferred | NR | Buhler et al. 1975 |
| Sick | Oregon | Fall 1971 | 2,M | 35.3 ±27.4 | 475 ±311 | NR | 28.5 ±2.1 | Inferred | NR | Buhler et al. 1975 |

TABLE 2. OC residues in California Sea Lion liver and brain ($\mu g \cdot g^{-1}$ lipid, mean ± SD).

| Sample type | Tissue | Site | Date | Number, sex | % Lipid | $p,p'-$DDE | Σ DDT | PCB | Reference |
|---|---|---|---|---|---|---|---|---|---|
| Full-term adult, 12 yr | Liver | Southern California | Spring 1970 | 4,F | 4.4 | 80–93% Σ DDT | 6.7 ±5.1 | 1.3 ±0.8 | DeLong et al. 1973 |
| Premature adult, 8 yr | Liver | Southern California | Spring 1970 | 6,F | 1.7 | 80–93% Σ DDT | 25 ±4 | 5.7 ±3.5 | DeLong et al. 1973 |
| Full-term pup | Brain | Southern California | Spring 1970 | 4,? | 4.8 | 80–93% Σ DDT | 1.2 ±1.1 | 0.2 ±0.05 | Delong et al. 1973 |
| Premature pup | Brain | Southern California | Spring 1970 | 6,? | 3.3 | 80–93% Σ DDT | 2.4 ±1.3 | 0.5 ±0.3 | DeLong et al. 1973 |

Two obvious questions arise: are these remarkably high OC residue concentrations, especially in blubber, accurate? If so, do they explain the prematurity and abortions observed in this population?

We can conclude that the OC residue data are substantially correct. There is enough internal consistency in the estimates of total OC concentrations, and in estimates of the fraction of DDT represented by $p,p'$-DDE as reported by three different groups to suggest that it is unlikely that they all made similar errors. LeBoeuf and Bonnell (1971) may have overestimated the DDT-group by not considering PCBs. However, if the latter PCB data are correct, their error in estimating $p,p'$-DDE would have been small, as the ECD response to PCBs is about one-tenth that of $p,p'$-DDE.

Whether premature births and abortions in the sea lion population can be attributed to the high OC concentrations is less clear. Interpretations of the OC data is hampered by the absence of any data describing the nutritional status of the "premature" group. If these animals had been emaciated as a result of some factor unrelated to OCs, but which may have caused prematurity, high blubber (and other tissue) OC concentrations would have been observed. The evidence relating OCs, *Leptospira*, and SMSV to prematurity can be summarized as follows: (a) high OC concentrations were associated with premature births, especially in younger females (DeLong et al. 1973; Gilmartin et al. 1976); (b) in one study, the prevalence of *Leptospira* infection of premature females was higher than that in normal animals (Smith et al. 1974b; Gilmartin et al. 1976); in another, *Leptospira* infection was not detected in premature animals (DeLong et al. 1973); (c) SMSV was present in all females, both premature and full-term (Gilmartin et al. 1976); (d) although high OC concentrations and *Leptospira* infections may have been correlated in females (see (a) and (b) above) there was no such correlation in males (LeBoeuf and Bonnell 1971; Buhler et al. 1975).

These points should be considered in the context of two other observations. First, the studies were made at the time, and near the site, of the Santa Barbara oil seep. Although a direct connection between the oil seep and the sea lion reproductive disorders can be ruled out (Brownell and LeBoeuf 1971), the spill may have contributed to some cumulative stress caused by environmental and microbial factors. Second (and as a final confusing note), another outbreak of *Leptospira* has been reported recently in this population, though apparently this was not associated with any unusual occurrence of abortions (Dierauf et al. 1985). Taking all the evidence together, I conclude that there are so many confounding factors in this series of observations that we cannot attribute prematurity specifically to the presence of higher OC concentrations or any other agent. On the other hand, we cannot exclude high OC levels as a factor contributing to reproductive disorders. The evidence is ambiguous.

## Gulf of Bothnia Ringed Seals

In the early 1970's, populations of both grey (*Halichoerus grypus*) and ringed (*Pusa hispida*) seals in the Northern Baltic were declining, even though hunting pressure had been reduced. Since some previous analyses had shown the presence of OCs and other pollutants in tissues from these animals (e.g. Jensen et al. 1969) Hook and Johnels (1972) suggested that the decline was associated with pollution. During the early 1970's, only small numbers of samples were analysed, but in the mid-1970's residue distribution in the Bothnian Bay ringed seal population was studied in detail. A strong correlation was found between blubber residue concentrations of PCBs above about 70 $\mu g \cdot g^{-1}$ lipid weight, and the presence of uterine occlusions (indicating reproductive problems) in sexually mature females.

Table 3 summarises these data. Holden (1969) had earlier found the DDT group at around 20 – 100 $\mu g \cdot g^{-1}$ in a sample of seven ringed seals from the Gulf of Bothnia (sex unspecified); PCBs were present but not quantified. Two ringed seals sampled from the Gulf of Bothnia in 1968 contained around 100 $\mu g \cdot g^{-1}$ DDT in blubber lipid and around 20 $\mu g \cdot g^{-1}$ of PCBs (Jensen et al. 1969). Olsson et al. (1974) reported that samples of ringed seals sampled in 1969–71 and then in 1972–73 from the Gulf of Bothnia contained DDT concentrations in the range of 200 and PCBs in the range of 100 $\mu g \cdot g^{-1}$. No

TABLE 3. OC residues in Bothnian Bay Ringed Seal blubber ($\mu g \cdot g^{-1}$ lipid, data as means or means ± SE). NR = not recorded, Calc. = author's recalculated data.

| Sample type | Date | Number, sex | % Lipid | Σ DDT | PCB | Reference |
|---|---|---|---|---|---|---|
| | May–Oct. 1968 | 2,? | 52,55 | 110,130 | 10,16 | Jensen et al. 1969 |
| <12 yr, Shot or drowned | 1969–71 | 13,? | NR | 200 ± 45 | 130 ± 29 | Olsson et al. 1974 |
| <12 yr, Shot or drowned | 1969–71 | 4,M | NR | 210 ± 63 | 160 ± 49 | Olsson et al. 1974 |
| <12 yr, Shot or drowned | 1969–71 | 2,F | NR | 125,130 | 66,85 | Olsson et al. 1974 |
| <12 yr, Shot or drowned | 1972–73 | 19,? | NR | 200 ± 37 | 100 ± 17 | Olsson et al. 1974 |
| Netted | 1973–74 | 40,F | NR | 110 ± 10 | 69 ± 4 | Helle et al. 1976a |
| Pregnant | 1973–74 | 15,F | NR | 75 ± 11 | 56 ± 6 | Helle et al. 1976a |
| Nonpregnant | 1973–74 | 26,F | NR | 130 ± 13 | 77 ± 5 | Helle et al. 1976a |
| Hunted | 1975 | 24,M | NR | 130 ± 18 | 100 ± 13 | Helle et al. 1976b |
| Normal, nonpregnant | 1975 | 8,F | NR | 100 ± 15 | 89 ± 11 | Helle et al. 1976b |
| Normal, pregnant | 1975 | 24,F | NR | 88 ± 10 | 73 ± 7 | Helle et al. 1976b |
| Nonpregnant, occlusions | 1975 | 29,F | NR | 130 ± 10 | 110 ± 8 | Helle et al. 1976b |
| Normal, nonpregnant | 1978–80 | 8,F | NR | 78 | 71 | Helle 1981 |
| Normal, pregnant | 1978–80 | 6,F | NR | 33 | 74 | Helle 1981 |
| Nonpregnant, occlusions | 1978–80 | 18,F | NR | 42 | 107 | Helle 1981 |
| Age 14 yr | 1980–81 | 9,? | NR | 54 ± 6 (Calc.) | 76 ± 11 (Calc.) | Helle and Stenman 1984 |
| Age 10 yr | 1982 | 10,? | NR | 51 ± 5 (Calc.) | 57 ± 10 (Calc.) | Helle and Stenman 1984 |
| Age 13 yr | 1983 | 12,? | NR | 58 ± 9 (Calc.) | 85 ± 12 (Calc.) | Helle and Stenman 1984 |

differences or trends in residue concentrations attributable to age or sex were observed, but this reflected the small sample size for a given sex in a given year.

The most comprehensive data set from the mid-1970's comes from a sample of 40 female ringed seals collected in 1973–74 and 133 males and females netted by hunters during 1974–75 in the Northern Gulf of Bothnia (Helle et al. 1976a, 1976b). The 24 males studied showed an increase in both DDT and PCBs with age, consistent with previous data; males also had consistently higher residue concentrations than most females. Among the females, pregnant animals and those with normal uteri did not differ significantly in blubber residue concentrations. In contrast, females with uterine occlusions (indicating some interference with implantation, or resorption of the developing foetus) had significantly higher ($P < 0.01$) levels of both DDT and PCBs than did either normal pregnant or nonpregnant females. However, the differences were not dramatic; females with uterine occlusions usually had blubber residue concentrations about 50% higher than did other females. As Reijnders (1980) has pointed out, nonpregnant females with uterine occlusions and those without were not compared. Examination of the data (summarised in Table 3) suggests that the mean DDT and PCB concentrations in these groups were barely different by 3 × SE. For comparison with other data sets, males and those females with uterine occlusions had mean residue concentrations around 130 $\mu g \cdot g^{-1}$ of DDT and about 100 – 110 $\mu g \cdot g^{-1}$ PCBs; normal females had around 90 – 100 $\mu g \cdot g^{-1}$ DDT and 70 – 90 $\mu g \cdot g^{-1}$ PCBs. Since females with uterine occlusions did not reproduce, and therefore did not excrete OCs during lactation, their blubber OC concentrations were similar to those in males.

Helle (1981) has assessed the temporal variation in OC residue concentrations in this population over the 1970's; although the data are not broken down by sex, there seems to be a fairly clear decline in DDT levels by the end of the decade, levels in the early to mid-70's were around 100 – 120 $\mu g \cdot g^{-1}$, but by 1978–80 were around 40 $\mu g \cdot g^{-1}$. PCBs, in contrast increased during the 70's to a maximum in 1977, and then began to fall, but not as dramatically as did DDT. These data are difficult to interpret since neither age nor sex data were provided.

The final data set from this population is summarized by Helle and Stenman (1984) and describes OC concentration trends during the early 1980's. Thirty-one animals, sampled over 1980–83 showed no trend in residue concentrations over this period, but levels were appreciably lower than in the mid-1970's, with DDT around 50 $\mu g \cdot g^{-1}$ and PCBs around 75 $\mu g \cdot g^{-1}$ lipid. The animals were not separated by sex, but the authors noted that the sex ratio was constant throughout the sampling period.

An isolated population of ringed seals from Lake Saimaa in eastern Finland has also been analysed for comparison with the Bothnian Bay population (Helle et al. 1983). Between 1977 and 1981, blubber lipid from these animals contained about equal amounts of DDT and PCBs (below 40 $\mu g \cdot g^{-1}$ of each) with traces of chlordane components. Concentrations of these residues in blubber increased with the animals' ages. Although this population also has declined during the last few years, the authors concluded that the decline could not be attributed to OC burdens.

Although the ringed seal has been the most intensively studied of the Baltic seals, similar distributions of OCs and of their putative effects, including uterine occlusions, have been observed in grey seals, *Halichoerus grypus* (Olsson 1978, 1986).

The Bothnian Bay ringed seal data are remarkably consistent internally, as is to be expected since most analyses were done by a single group of analysts. The data appear to make two points quite clearly: (a) the occurrence of uterine occlusions is well correlated with blubber PCB concentrations above about 70 $\mu g \cdot g^{-1}$ (as estimated by the total envelope method)? in Bothnian Bay ringed seals; (b) over the period from the early 1970's to the early 1980's residue concentrations in these animals have declined appreciably — though perhaps not quite enough to eliminate concern about the impact of surviving residues on reproduction.

However, a critical examination of the data leaves some questions to be answered. Consider first the conclusion that PCB concentrations above about 70 $\mu g \cdot g^{-1}$ in blubber lipid are associated with reproductive defects. This is based on comparisons of nonpregnant and normally pregnant females; the former contained PCB and DDT concentrations about 50% higher than the latter. While this difference may be statistically significant, its physiological significance might be questioned. It is now well known that residue concentrations are inversely related to blubber thickness, and a 50% reduction in blubber thickness or lipid content would cause the observed concentration increase — although the total residue burden in the affected seals would not differ. We have observed a 30% change in blubber thickness in the same population of western Arctic ringed seals sampled in different years (Addison et al. 1986) and this illustrates the importance of normal physiological processes — i.e. processes unrelated to the presence of OCs, in controlling condition, and hence blubber OC concentrations. It is unfortunate that some measure of condition was not published as part of the record of the Bothnian Bay ringed seal studies.

In the absence of information about the condition of the Gulf of Bothnia ringed seals, we cannot conclude that females with uterine occlusions had higher body burdens of OC residues. The higher residue concentrations associated with reproductive problems may simply be a result of some other physiological factor, rather than a cause of the reproductive problem.

One final question about the ringed seal data set concerns the analysis of trends in PCB residue concentrations. The recent data (Helle and Stenman 1984) are based on analyses by capillary GC and MS confirmation by selected ion monitoring (Moilanen et al. 1982). In our experience (Addison et al. 1986) capillary column GLC of PCB congeners in environmental samples leads to estimates of total PCBs about 20 – 25% of those estimated by the "total envelope" method, because the distribution of congeners in the samples is simpler than that in standard mixtures. However, Helle and Stenman (1984) do not discuss what corrections they have made to the PCB estimates by the Moilanen et al. (1982) method to make the later data comparable with those obtained by the total envelope method during the mid-1970's. Thus, it is difficult to assess whether the trends inferred from comparison of the mid-1970's and early 1980's data really exist. However, the reported trends are generally similar to those seen in other seal populations in Canada (Addison et al. 1984, 1986).

To conclude, the Gulf of Bothnia ringed seal data suggest that PCB blubber lipid concentrations over about 70 $\mu g \cdot g^{-1}$ (and/or higher DDT concentrations) are associated with reproductive defects caused by uterine occlusions. Whether the high OC residues cause these effects, or whether they are a parallel result of some other cause is not yet clear. Finally, the reported trends in PCB concentrations over the late 1970's require careful evaluation.

TABLE 4. OC residues in Waddensee Harbour Seal blubber ($\mu g \cdot g^{-1}$ lipid; means or means and ranges). NR = not reported, GM = geometric mean, CL = confidence limits, calc. = author's recalculated data.

| Sample type | Site | Date | Number, sex | % Lipid | *p, p'* – DDE | Σ DDT | PCB | Reference |
|---|---|---|---|---|---|---|---|---|
| Adult (most found dead) | Dutch Waddensee? | 1970–71 | 5,? | 54 (19–68) | 11.3 (Calc.) | 17.6 (Calc.) | 2722 (Calc.) | Koeman et al. 1972 |
| Shot or stranded, 6–8 yr | German Waddensee | 1974–76 | 4,? | 96.3 (93.3–99.1) (Calc.) | 2.4 (1.2 – 3.1) (Calc.) | 6.5 (4.8 – 8.1) (Calc.) | 171 (33–266) | Drescher et al. 1977 |
| Stranded adults | German Waddensee | 1975–76 | 6,? | NR | 5.0 (2.4 – 8.8) | 8.5 (3.7 – 15.2) | 76 (41 – 123) | Reijnders 1980 |
| Stranded adults | Dutch Waddensee | 1975–76 | 8,? | NR | 26.6 (3.8 – 72) | 47.3 (6.6 – 178) | 701 (87 – 1447) | Reijnders 1980 |
| Stranded | Dutch Waddensee | 1972–81 | 137,? | NR | NR | NR | 89 (GM) 95% CL: 72–110 | Van der Zande and De Ruiter 1983 |
| Stranded | Dutch Waddensee | 1970's | 4,F and 3,M | 85.6 ± 11.0 (SD) (Calc.) | 8.8 (0.6 – 22.3) (Calc.) | 12.4 (0.6 – 28.2) (Calc.) | 231 (24 – 640) (Calc.) | Duinker et al. 1977 |

## Dutch Waddensee Harbour Seals

Like the Gulf of Bothnia ringed seals, the numbers of Dutch Waddensee harbour seals (*Phoca vitulina*) have declined during the past few decades (Reijnders 1980). This decline has been associated with high OC residue levels, particularly those of PCBs. The Dutch Waddensee harbour seals cannot be separated into "normal" and "reproductively defective" groups on the basis of their residue concentrations, but they can be compared with German and Danish Waddensee populations which supposedly have lower residue concentrations and show no such reduction in numbers. The pathological symptoms like uterine occlusions and stenoses which have been found in Baltic ringed and grey and occasionally harbour seals have not been reported in the Waddensee animals.

Blubber OC residue concentrations are summarised in Table 4. German Waddensee samples were taken during 1974 and 1976 from the Schleswig–Holstein area, and were separated into "healthy," "sick," or "found dead" categories (Drescher et al. 1977). PCBs ranged up to about 600 $\mu g \cdot g^{-1}$ blubber lipid (means around 150 $\mu g \cdot g^{-1}$, varying with the animals' age) and DDT up to about 30 $\mu g \cdot g^{-1}$ (means around 10 $\mu g \cdot g^{-1}$). PCB and DDT concentrations were themselves highly correlated, and PCB concentrations were inversely correlated with blubber thickness. An additional sample of harbour seals from the Waddensee and Baltic coasts of Schleswig–Holstein (Harms et al. 1978) showed a roughly similar range of residue concentrations.

Several data sets describe OC residues in Dutch Waddensee harbour seals. First, Koeman et al. (1972) reported PCBs at concentrations of several hundred $\mu g \cdot g^{-1}$ in blubber with DDT in the 10 $\mu g \cdot g^{-1}$ range. However, the ranges quoted are very wide, and extractible blubber lipid was relatively low, suggesting that the animals may have been in poor condition; indeed, some had been found dead. Reijnders (1980) summarized analyses of both German and Dutch Waddensee harbour seals, collected in 1975 and 1976. The German and Danish samples contained PCBs, measured as decachlorobiphenyl, at concentrations of up to 340 $\mu g \cdot g^{-1}$, and DDT at up to 47 $\mu g \cdot g^{-1}$. Mean concentrations were similar to those reported by Drescher et al. (1977) at around 100 $\mu g \cdot g^{-1}$ for PCBs and around 12 $\mu g \cdot g^{-1}$ for DDT. Surprisingly, juvenile and subadult specimens seemed to have generally higher concentrations than did the adults; sexes were not recorded. Juveniles and adults from the Dutch Waddensee contained (respectively) PCBs at mean concentrations of 130 and 700 $\mu g \cdot g^{-1}$ and DDT at mean concentrations of 30 and 47 $\mu g \cdot g^{-1}$. Thus, the Dutch Waddensee samples contained both PCB and DDT concentrations appreciably higher than those from Germany and Denmark. However, sample sizes were generally small and ranges of concentrations were very large, with the result that the spatial differences were significant only in the case of adult PCB and *p,p'*-DDT concentrations. Levels of other trace OCs were also measured and some of these, like dieldrin levels in adults, also differed significantly; however, their absolute concentrations were only about 1% or less of those of the DDT-group or the PCBs. (Apropos of methods, the estimation of PCBs as decachlorobiphenyl involves perchlorination with $SbCl_5$, a reaction which may not proceed quantitatively: Armour 1975; Trotter and Young 1975. However, the error introduced by this method is probably no greater than that from the more subjective estimate of PCBs by comparing the total PCB envelope in an environmental sample with that in a standard mixture).

Van der Zande and de Ruiter (1983) analysed samples of belly blubber from harbour seals found dead on the Dutch Waddensee coast between 1975 and 1981; these samples are comparable with the Dutch Waddensee samples described by Reijnders (1980). Van der Zande and de Ruiter (1983) reported the geometric mean of PCB concentrations (determined by an elaborate peak-summing method) in blubber lipid as being around 90 $\mu g \cdot g^{-1}$ — very close to the values recorded in German Waddensee samples (Drescher et al. 1977; Reijnders 1980). Van der Zande and De Ruiter (1983) also found that younger animals (<4 yr) had lower PCB concentrations than those over 4 yr, and that there seemed to be a general decline in PCB levels between 1975 and 1981. They also reported a negative relationship between PCB concentration and blubber thickness, and a positive relationship between PCB concentration and age (in both males and females). This is an interesting data set, not only because of its size and the depth in which it has been interpreted, but because of its similarity and relevance to Reijnders' (1980) data. Thus, Van Der Zande and De Ruiter (1983) reported mean blubber thickness as being around 1 – 2 cm in most cases. This is about half the blubber thickness we would expect in healthy harbour seals in eastern Canada, and it suggests that these stranded dead seals were in poor condition. (In this context, Brodie and P'åsche (1982) have shown

the rapid metabolism of tissue in grey seals with these reduced blubber thicknesses.) Van der Zande and De Ruiter (1983) also found a steep slope for the negative regression of PCB concentration on blubber thickness, and this emphasizes the need to consider condition in making temporal or spatial comparisons between residue concentrations in different samples. They also stated explicitly that stranded animals had less blubber than some healthy specimens drowned in a net; PCB concentration in the "healthy" specimens appear slightly lower than in stranded animals. We may infer from these observations that Reijnders' (1980) samples (also of stranded animals) may have been partially emaciated and therefore may have represented a wide range of condition and blubber thickness. This, together with the unknown variation in age and sex in these animals, would explain the wide variance in the data.

The data of Van der Zande and De Ruiter (1983) therefore suggest that residue burdens in stranded harbour seals may appear unusually high, because residue concentrations have not been interpreted in the light of information about condition and blubber thickness.

(Incidentally, the reason that Van der Zande and De Ruiter (1983) found a positive relationship between PCB concentrations and age in female seals is probably that most of their samples were younger than 4 yr; they would not have been sexually mature, and so lactation would not yet have begun to contribute to the clearance of OCs from their blubber.)

The most recent attempt to assess the impact of OCs on seal reproduction has been Reijnders' (1986) report of an experiment in which harbour seals were fed natural diets over approximately 2 yr containing different contents of PCBs and *p,p'*-DDE. The "reference" group of 12 female seals had an average daily intake of 0.22 mg of PCBs and 0.13 mg of *p,p'*-DDE derived from a diet based on Atlantic mackerel (*Scomber scombrus*) and the "experimental" group (also 12 females) received 1.5 mg of PCB and 0.4 mg of *p,p'*-DDE daily from a diet based on Waddensee plaice (*Pleuronectes platessa*). Three males on the reference diet alternated between both groups during the mating period. No differences occurred in circulatory hormone levels between the two groups of females, but females on the "Waddensee" diet had significantly lower reproductive success. In a later paper, Boon et al. (1987) have summarized PCB congener dynamics in these animals. Mean PCB concentrations in blood were 25 – 27 $\mu g \cdot g^{-1}$ lipid (depending on year of sampling) in the "Waddensee" group and 5.2 – 11 $\mu g \cdot g^{-1}$ lipid in the "Atlantic" group; these differences were usually statistically significant.

This is the first experimental (as opposed to correlative) evidence that OCs may affect seal reproduction, but even this technically difficult experiment did not yield unequivocal conclusions, as the diets differed in lipid and therefore caloric content. Although this difference "was compensated for by a high daily intake" it implies that the two groups were on a nutritionally different regime; the extent to which this may affect reproductive success is not stated.

In summary, interpretation of the Waddensee harbour seal data is difficult because the data are based mainly on studies of stranded animals which vary widely in condition (and hence in blubber residue concentrations), and because age, sex, and condition were often unrecorded. Nevertheless, there appears to be a difference in blubber residue concentrations of PCBs and the DDT group between Dutch Waddensee animals (which accumulate pollutants probably introduced via the Rhine) and German and Danish Waddensee animals, and this is associated with differences in reproductive success. The experimental feeding results certainly suggest that some Waddensee dietary component contributes to reproductive failure in harbour seals.

## Saguenay Estuary Beluga Whales

It is difficult to discuss this in any detail since few reports on the subject are available yet in the open literature.

Stranded beluga whales (*Delphinapterus leucas*) from the Gulf of St. Lawrence contain high blubber PCB concentrations, and these have been postulated to contribute to the decline of this population (Massé et al. 1986; Martineau et al. 1987). Blubber PCB concentrations measured by reliable methods (Desjardins et al. 1983) ranged up to several hundred $\mu \cdot g^{-1}$ wet weight (Table 5) and showed an increase with age in both sexes. DDT-group concentrations also reached several hundred $\mu \cdot g^{-1}$ in some samples. In general, residue concentrations were not related to blubber thickness. Stranded animals represent a special sample; the animals may have died of causes unrelated to OC contamination and the physiological processes which appear to control OC distribution in other mammals may be impaired. The authors pointed out that blubber thickness in their sample was generally lower than that measured in the same population 50 yr ago, but stated that blubber thickness is highly variable in this species. Residue concentrations in liver and kidney were also reported and these also cover a very wide range.

Some comparable data are available from apparently healthy belugas taken by hunting in the western Arctic (Addison and Brodie 1973). PCBs were not detected in these samples, but DDT represented about 3 $\mu \cdot g^{-1}$ blubber wet weight, and less than 0.05 $\mu \cdot g^{-1}$ liver wet weight. However, we know from other studies that the OC residues in western Arctic marine mammals are about one-tenth or less than those in the Gulf of St. Lawrence (Addison and Smith 1974; Addison et al. 1973, 1984, 1986). If we allow for that factor of 10 in comparing blubber and liver wet weight OC concentrations we find that those from the Gulf of St. Lawrence are higher than expected from the western Arctic samples, but not dramatically so. However, declines in general OC contamination from the early 70's to the mid-80's may increase the difference. Furthermore, the concentrations quoted from the Gulf of St. Lawrence stranded belugas are not much different from those reported in various species of stranded whales found on the coast of France (Alzieu and Duguy 1979); blubber PCB concentrations in the latter were in the range of several hundred, and DDT around 100 $\mu \cdot g^{-1}$

TABLE 5. OC residues in blubber of Beluga whales (ppm wet weight, means and ranges). NR = not recorded, ND = not detected.

| Sample type | Site | Date | Number, sex | % Lipid | *p, p'* – DDE | Σ DDT | PCBs | Reference |
|---|---|---|---|---|---|---|---|---|
| Stranded | Gulf of St. Lawrence | 1982–85 | 16,M; 8,F; 1 Unknown | NR | | 60 (1.1 – 225) | 146 (5.7 – 576) | Martineau et al. 1985 |
| Hunted | Mackenzie Delta, N.W.T. | 1972 | 7,? | ca. 93–94 | ca. 1 | ca. 3 | ND | Addison and Brodie 1973 |

wet weight. Liver and kidney OC concentrations in the stranded French specimens were in the same range, or even higher, than those in the Gulf of St. Lawrence beluga.

These comparisons suggest that OC residue concentrations in the Gulf of St. Lawrence are relatively high, as compared with other species from the same area, but are perhaps not out of line with samples from other stranded whales. Considering the difficulty of interpreting the wide range of residue concentrations found in these animals and the range of condition and ages they cover, it is difficult to conclude that any decline observed in this population could be attributed specifically to their OC residue concentrations. However, the generally increased industrialization of the area, together with increased shipping, may have led to some deterioration of habitat which could have affected the animals.

## General Discussion and Conclusions

Do OC residues affect reproduction in marine mammals? In the case of the California sea lions, the evidence is too ambiguous to yield a simple answer; in the Gulf of St. Lawrence beluga, too few data exist to lead to any conclusion. Some connection between residues and reproduction is implied by correlative evidence from the Baltic ringed seals and by both correlative and experimental evidence from Waddensee harbour seals. However, interpretation of the residue data is often complicated by the absence of relevant biological data such as blubber thickness, which may be affected by processes such as starvation. A further confounding factor is that generally increased industrialization and shipping may have led to some deterioration of habitat which could have stressed many of the marine mammal populations.

Field observations of a connection between OC residues and reproduction in wild seal populations are supported by laboratory studies on other mammals, where a cause–effect relationship between PCB exposure and reproduction has been found. Mink (*Mustela vison*) is the experimental model used most often because it experiences delayed implantation of the blastocyst, as do seals and other marine mammals. Mink exposed adventitiously or experimentally to PCBs in their diet generally have fewer implantations and show reduced birth rates with smaller offspring than control animals (Aulerich and Ringer 1977; Jensen et al. 1979; Bleavins et al. 1980). Some other laboratory mammals show related responses (Fuller and Hobson 1986). However, the biochemical processes leading to these effects have not been identified. It might be surmised that if PCB exposure changes hepatic microsomal mono-oxygenase activity, this may in turn disrupt steroid metabolism (since steroid hormones are among the natural substrates for this enzyme system) but a detailed chain of biochemical events which would explain the whole organism response has not been proposed. And although some experimental treatments of PCB have led to disrupted steroid hormone metabolism (Fuller and Hobson 1986) Reijnders (1986) reported no change in circulatory hormone levels in female harbour seals with reduced birth rates. Given the complexity of PCB mixtures and the variety of effects that they may produce singly or in combination, and considering our ignorance of the basic biochemistry of normal marine mammal reproduction, it is not surprising that we cannot identify a biochemical basis for this apparent effect of PCBs. The problem is further complicated by the fact that any proposed mechanism would have to explain the different effects observed in ringed and harbour seals.

Where do we go from here? Recent analyses suggest that some OC residue concentrations are declining in some marine mammal populations (e.g. Helle and Stenman 1984; Addison et al. 1984, 1986). If this is so, field observations of the (putative) impact of OCs on reproduction may be less frequent in the future. If a conclusive demonstration of the connection between OC residues and reproduction is required, it would be better approached experimentally. At present, the most useful focus of such studies might be on the interactions between OC and the hormonal control of reproduction, especially at the implantation stage. Since it would be difficult to approach this experimentally using seals, the mink might be used as an experimental model.

In summary, high OC residue concentrations (especially of PCBs) are associated with reproductive disorders in two seal populations, but not convincingly so in sea lions or beluga whales. Enough evidence exists from laboratory studies on other mammals to expect that PCBs could affect reproductive processes especially in female mammals. The biochemical mechanism of this might be studied using mink as an experimental model.

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# CORRECTIONS SUR RÉCENTES PUBLICATIONS

VOLUME 45, No. 6 — review by E. M. Hallerman and J. S. Beckmann: *DNA-level polymorphism as a tool in fisheries science*.

Page 1078: M. Castelli was not properly credited for her original idea of utilizing DNA fingerprinting techniques to document the occurrence of successful gynogenesis (see Georges et al. 1988, Cytogonet. Cell Genet. 47: p. 130). The authors regret this error.

# ANNOUNCEMENTS/AVIS

## Symposium on Multispecies Models Relevant to Management of Living Resources

*The Hague, Netherlands, 2–4 October 1989*
*Organized by The International Council for the Exploration of the Sea ICES*

The purpose of the Symposium is to (1) encourage quantitative analysis of biological and technological interactions relevant to management of living resources, (2) provide a forum for comparison of approaches applied both within and beyond ICES primary area of interest, (3) provide a summary of the "State of the Art".

The Symposium, for which there is no registration fee, is open to all interested scientists who announce their participation in advance. Participants are requested to inform the general secretary by not later than 31 August 1989. Information regarding the venue and arrangements for the Symposium hotel accommodation, etc. in The Hague will be provided by the ICES Secretariat following receipt of such notification.

Co-conveners: Dr. M. P. Sissenwine, Northeast Fisheries Center, NMFS/NOAA, Woods Hole, MA 02543, USA. Dr. N. Daan, Netherlands Institute for Fishery Investigations, Postbus 68, 1970 AB Umuiden, The Netherlands.

For administration purposes please contact ICES Secretariat General Secretary ICES/CIEM Palaegade 2–4 DK-1261 Copenhagen K Denmark.

## Symposium sur l'Application de Modèles Polyvalents à la Gestion des Ressources Biologiques

*La Haye (Pays-Bas), du 2 au 4 octobre 1989*
*organisé par Le Conseil international pour l'exploration de la mer CIEM*

Buts du symposium (1) favoriser l'analyse quantitative des interactions biotiques et technologiques afférentes à la gestion des ressources biologiques, (2) servir de tribune où l'on pourra comparer les approches appliquées au domaine d'intérêt principal du CIEM et à d'autres domaines, (3) brosser un tableau des techniques de pointe.

Tous les scientifiques intéressés sont admissibles, mais ils doivent en informer les organisateurs au préalable. Il n'y a aucuns frais d'inscription. Les participants sont priés d'aviser le secrétaire général au plus tard le 31 août 1989. Après réception de cet avis, le secrétariat du CIEM fournira des renseignements sur le lieu exact de la réunion et les chambres d'hôtel.

Autres convocateurs Dr. M. P. Sissenwine, Northeast Fisheries Center, NMFS/NOAA, Woods Hole, MA 02543, USA. Dr. N. Daan, Netherlands Institute for Fishery Investigations, Postbus 68, 1970 AB Imuiden (Pays-Bas).

Pour obtenir des renseignements à des fins administratives, prière de s'adresser au Secrétaire général CIEM/ICES Palaegade 2–4 DK-1261 Copenhague K Danemark.

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